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EDITORIAL COMMITTEE

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STEPHEN ALFRED FORBES

WILLIAM TRELEASE

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10187





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# A REVISION OF THE CESTODE FAMILY

## ERRATA

Page 29, line 3, for 'Bendict' read 'Benedict'.

" 70, line 4, for '*P. longicollis* (Rud.)', read '*P. longicollis* (Zeder)'.

" 71, line 2 from bottom, for '*Lota vulgaris*' read '*Lota vulgaris*'.

" 72, line 2, for '*Coregonus fera*', read '*Coregonus fera*'.

" 77, line 29, for '*P. longicollis* (Rud.)', read '*P. longicollis* (Zeder)'.

" 78, line 7, for '*P. agonis* Barbieri', read '*P. agonis* (Barbieri)'.

" 105, line next to bottom, for '*P. oscellatus*', read '*P. ocellatus*'.

" 134, lines 11, 13, 15, for *T. hemisphaerica*', read *T. hemispherica*'.

" 135, lines 6 and 18, page 143, lines 8 and 10, page 176, line 23, for '*P. hemisphaericus*', read '*P. hemisphericus*'.

" 144, line 3 of table, for '*Salmoides*', read '*salmoides*'.

" 262, last line, for '*seg-*', read '*segment*'.

" 283, last line of table, for *O. trimeresurus*', read *O. trimeresuri*'.





A REVISION OF  
THE CESTODE FAMILY  
PROTEOCEPHALIDÆ

BY

GEORGE ROGER LA RUE

Contributions from the  
Zoological Laboratory of the University of Illinois under the direction of  
Henry B. Ward, No. 33

THESIS

Submitted in Partial Fulfilment of the Requirements  
for the Degree of Doctor of Philosophy  
in Zoology in the Graduate School  
of the University of Illinois

1911



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## INTRODUCTION

Several years ago while studying under Professor Henry B. Ward at the University of Nebraska the writer began an investigation of a cestode parasitic in *Amblystoma tigrinum* (Green). That investigation resulted in a paper (La Rue 1909) in which a number of points in the anatomy of Proteocephalids were cleared up and certain problems were outlined for investigation at an early date. In the meantime the writer became interested in the large number of Proteocephalids which Professor Ward had secured by work in the field and by exchange. The writer had also made some collections. A preliminary study of the available material by the writer was convincing to Professor Ward that a more complete and comparative study of the group was desirable and that the results of such a study would prove of value to helminthologists, not only of America but also in Europe. Such a study seemed more desirable since but two comparative studies of the group had been made in more than fifteen years, the first by Riegenbach (1896) mostly on the species infesting fish, and the second by Schwarz (1908) wholly on the species infesting snakes and reptiles. The fact that very little had been done on the genus by American investigators furnished an added incentive to undertake the work.

At Professor Ward's suggestion and under his direction the writer undertook an investigation of the genus which would be comprehensive in scope and at the same time comparative. For this purpose Professor Ward augmented the material already at hand by securing the loan of alcoholics and prepared slides from several European and American investigators and from the collections of the Smithsonian Institution and the Bureau of Animal Industry at Washington. Unfortunately specimens of certain material could not be secured either because it had been lost or because it could not be removed from the collections.

The lack of some of this material has caused the writer to change the plan of the paper somewhat. Instead of making a fresh study of each species it has been necessary in describing certain species to depend on the data secured from the literature. These data have been recombined and quotations have been made, sometimes quite extended, while

original drawings which were found useful in presenting the characters and structures of the species have been copied and used in the new account. Possibly it may seem that a consideration of these species might have been omitted without apparently having great effect on the value of the work. The writer found however that serious errors had been made in determination and upon these mistaken determinations identification of other species had been made dependent. The only way of escape from the tangle was to consider every species in the family.

In order that the work might be of more value to many of the American investigators to whom large numbers of the older works of the European writers are unavailable and for the purpose of comparison large extracts from these older writings have been quoted verbatim. For these reasons also the number of drawings copied is larger than at first glimpse seems necessary. The writer has been compelled however to omit because of lack of space many extracts and many drawings which would add to the value of the work. In working over the large literature on the subject an attempt was made to secure every important paper. Some less important papers are known to have been omitted.

Thanks are due to the following investigators who at the request of Professor Ward so kindly sent prepared slides or alcoholics from their valuable collections for study and comparison: Professor Fritz Zschokke, University of Basle, Professor Corrado Parona, University of Genoa, Professor Max Braun, University of Königsberg, Professor K. M. Levander, Helsingfors, Finland, Professor Anton Collin, University of Berlin, Professor A. E. Shipley, Christ's College, Cambridge, Professor Fr. Sav. Monticelli, University of Naples, Professor O. Fuhrmann, University of Neûchatel, Dr. C. W. Stiles, Hygienic Laboratory, Washington, D. C., Dr. B. H. Ransom, Bureau of Animal Industry, Washington, D. C., Professor Edwin Linton, Washington and Jefferson College, Professor A. J. Smith, University of Pennsylvania, Professor L. T. Hankinson, Charleston, Ill. Mr. E. G. Davis of Lincoln, Nebr., and Mr. Herman Douthitt of Sulphur, Oklahoma, have also very kindly furnished material for study. Thanks are due Mr. S. Fred Prince for re-drawing many of the figures from other works and for making my pencil sketches into the finished drawings.

To the United States Bureau of Fisheries and to its corps of scientific workers I am indebted for encouragement and assistance in many ways, especially in securing valuable material from various sources.

To Professor Henry B. Ward my sincerest thanks are due for the use of his extensive collections, for the use of his library, and also for securing for my use many rare specimens and rare books. His interest and co-operation have given me the inspiration to complete the work.

## HISTORICAL DATA

Rudolphi (1808-10) collected together the results of the systematic labors of helminthologists up to that time. His work is very complete and in it are to be found the diagnoses, synonymy and descriptions of the species of this genus that were known at that time. These species are included in the genus *Taenia* Linnaeus 1758. It is to be noted that Rudolphi renamed certain of these species which had been previously established by other investigators. Later Rudolphi (1819) brought down to date a summary of the investigations of preceding helminthologists.

Some of the early investigators, other than Rudolphi, who reported species now included in the genus *Proteocephalus*, were Goeze, O. F. Müller, Pallas, Gmelin, Batsch, Schrank, Zeder, Bloch, and Froelich. Many of their descriptions and diagnoses were very short. Only a few were accompanied by drawings. It is needless to say that the works of these early investigators are almost entirely concerned with the study of external characters. There were no more important works which have to do with this group of cestodes until the time of Dujardin (1845) and Diesing (1850). These investigators listed several new species and new host species.

Investigators up to the time of Monticelli (1891) with the exception of Weinland (1858) considered this group of fish cestodes to belong to the genus *Taenia*. The latter author proposed the name *Proteocephalus* which will be discussed later and the former proposed the name *Tetracotylus*. It was von Linstow (1891) who first pointed out that the fish species made up a closely related group within the genus *Taenia*. He made the first careful study of one of the species of this group.

Monticelli (1891) made a careful study of the group and pointed out several misinterpretations relating to the genital organs. He first showed the true relationships of the organs in the interovarial space. His work was largely based on *Taenia coryphicephala* with which he compared other species. In all he listed 20 species belonging to his genus *Tetracotylus*. Of these species some were from snakes. For a more complete discussion of that work see the description of *Monticellia* (*Tetracotylus*). Since this work of Monticelli, Lönnberg (1894) proposed the genus *Ichthyotaenia* and in this genus many species have been included. The range of hosts includes amphibians, snakes, lizards, and all the larger groups of freshwater fish.



In 1899 Monticelli recognized that *Tetraphothrium gerrardii* Baird, a parasite of the Boidae, belonged in this family of cestodes but that it should be separated from the species of *Proteocephalus*, and for this species he proposed the genus *Crepidobothrium*. In 1903 von Linstow proposed the genus *Acanthotaenia* to include a spiny headed *Proteocephalid* from Varanus. This genus was later emended by Johnston (1909) who placed three other species in it, all from Varanidae.

It has been found necessary to restrict the genus *Proteocephalus* by removing from it the species of amphibian and ophidian *Proteocephalids*. These make a fairly homogeneous group for which the writer proposed the name *Ophiotaenia* La Rue 1911 with *Ophiotaenia perspicua* La Rue as the type species.

#### SYNONYMY

Weinland (1858:53) proposed the genus *Proteocephalus* and named as its type *Taenia ambigua* Dujardin. *Taenia filicollis* and *Taenia dispar* were also included under this genus.

Lönnberg (1894:801-803) proposed the generic name *Ichthyotaenia* and listed as members of this genus: *I. filicollis* Rud., *I. ocellata* Rud., *I. longicollis* Rud., *I. torulosa* Batsch, and *I. coryphicephala* Monticelli. Since Lönnberg named *I. filicollis* first in his list that name is to be considered the type of his genus and has been so designated by Hall (1910). Thus he made *Ichthyotaenia* a synonym of *Proteocephalus* unless *T. filicollis* Rud. is generically different from *T. ambigua* (Dujardin). On this point Railliet (1899) says: "Comme cette espece (*Taenia ambigua* Duj.) rentre nettement dans le genre *Ichthyotaenia* il est evident que le premier nom (*Proteocephalus*) doit etre repris." The validity of the names *Proteocephalus* Weinland or *Ichthyotaenia* Lönnberg then depends on the species *T. ambigua* Dujardin and *T. filicollis* Rud. The first named species was fairly well described and measurements of diagnostic value were given by Dujardin (1845). This species has since been well described and figured by G. Schneider and later by the writer using Schneider's material which agrees almost perfectly with Dujardin's description of *T. ambigua*.

*Taenia filicollis* Rud. is not a synonym of *Taenia ocellata* Rud., and consequently, of *Taenia percae* Müller, as Kraemer, Riegenbach, Benedict, Railliet, and others have thought. That belief was founded on a mistaken identification by Kraemer (1892). Since Dujardin (1845) there have been but few records of examinations of *Gasterosteus*. One of these records is by Lönnberg, another by Schneider. They examined *Gasterosteus pungitius*, while the type host of *T. filicollis* is *Gasterosteus*

*aculeatus* and so far as the writer can discover there have been almost no records of collection of parasites from that host since Dujardin. The diagnoses of *Taenia filicollis* much resemble those of *Taenia ambigua*. Dujardin however evidently considered these two species as different for he records both. At the present time but a single species is well known from Gasterosteus, viz. *Proteocephalus ambiguus* (Dujardin). The writer considers however that *P. ambiguus* is identical with *P. filicollis* (Rud.) and hence the genera *Proteocephalus* Weinland and *Ichthyotaenia* Lönnberg being based on the same species are synonyms and the earlier name should be retained.

The synonymy of the name *Tetracotylus* Monticelli (1891) has not yet been discussed. This name was based on the description of *Taenia coryphicephala* altho Monticelli failed to designate it as the type species. Braun (1894-1900) stated that this genus was based on *T. coryphicephala* and this action was considered by Hall (1910) to be tantamount to the designation of a type. Braun regards *Tetracotylus* to be a synonym of *Ichthyotaenia* which makes it a synonym of *Proteocephalus* provided that the type of *Tetracotylus* belongs in the same genus with *Taenia filicollis* (Rud.), the type of *Proteocephalus*. That *Tetracotylus coryphicephala* does not belong to the same genus with *Proteocephalus filicollis* has been shown by the writer in the descriptive study of the former species (vide infra). Moreover the writer has shown that this form does not belong with any genus of cestodes at present known. It is then necessary to examine into the status of the name *Tetracotylus* as a generic name for *Taenia coryphicephala*.

The availability of *Tetracotylus* has been questioned because of the name *Tetracotyle* Filippi (1854). These two names are not spelled alike and are therefore not homonyms. Braun (1894-1900) suggests that *Tetracotylus* has been used for *Tetracotyle*. If such improper use has been made of the former name prior to the time when Monticelli proposed it then *Tetracotylus* has been rendered unavailable. The writer has not been able to find evidence of such improper use, yet because of Braun's statement of the fact and his objection to the use of the name the writer has proposed the name *Monticellia* in honor of Professor Monticelli who has done so much for our knowledge of this group, as a name to take the place of the invalidated *Tetracotylus*. The type of this genus is *Monticellia coryphicephala* (Monticelli).

The genus is to be defined thus: *Monticellia* La Rue: Head small, globose, without folds or lappets of tissue encircling suckers. Suckers sessile and without accessory areola. No rostellum. Testes, vitellaria and uterus entirely outside of the inner longitudinal muscle-sheath. Vitellaria composed of scattered follicles which form broad

lateral fields. Testes numerous, forming a single broad dorsal field between vitellaria. Uterus ventral, with many lateral pouches. Genital pore marginal, irregularly alternating. Ovary bilobed and situated partly within and partly outside the inner muscle-sheath. Sexual organs in general as in Proteocephalidae. In Siluridae. The type of the genus is *Monticellia coryphicephala* (*Tetracotylus coryphicephala* Monticelli).

The position of this genus in the order Tetracotylidae is difficult to determine. It apparently does not belong to any of the families as now defined therefore the writer suggests for it the family name Monticellidae with the following characters: Head small. Suckers sessile and without accessory areola. Internal anatomy as in the type genus Monticellia.

There still remains the question as to whether the name Proteocephalus is available. That name has been objected to on account of the name Proteocephala suggested by de Blainville (1828) for a cestode family. These two names are not homonyms and it is agreed that the use of a name to designate a family does not invalidate it for use subsequently as a generic name. The writer therefore retains the name Proteocephalus Weinland as the generic designation for the genus of which *Taenia filicollis* Rud. is the type.

Having determined that *Monticellia coryphicephala* (Monticelli) does not belong in the family Proteocephalidae because of its peculiar organization, it is necessary to redefine that family thus: Family Proteocephalidae: Heads small. Suckers sessile and without accessory areola. Fifth sucker functional, vestigial, or lacking. No rostellum. Genital organs in general as in other Tetracotylidae. Genital pores marginal, irregularly alternating. Vitellaria lateral, follicular, follicles closely grouped about a central conducting tubule. Ovary bilobed, posterior. Oöcapitulum, oötype, shell gland, uterine passage present. Uterus with lateral outpocketings and one or more preformed ventral uterine openings. Vitellaria, testes, ovary and uterus within the inner longitudinal muscle-sheath.

Habitat: In fresh-water fish, amphibia, and aquatic reptiles.

In this family belong the following genera which are here defined:

(1) *Proteocephalus* Weinland 1858

With characters of the family. Head globose or conical, flattened dorsoventrally. No rostellum. No spines or hooks. No fold of tissue encircling base of head or enfolding suckers. Suckers circular or oval. Fifth sucker functional or vestigial, rarely lacking. Testes in a broad field between vitellaria. Parenchyma with close meshes. Musculature well developed. Eggs with three membranes. Habitat: In fresh-water fish.



Type species: *Proteocephalus filicollis* (Rudolphi)

Syn.: *Proteocephalus ambiguus* (Dujardin)

(2) *Choanoscolex* La Rue 1911

With characters of family. Head conical with a fold of tissue at the base partially covering suckers. No rostellum, no hooks, no spines. Genital organs as in *Proteocephalus*. Habitat: In Siluridae.

Type species: *Choanoscolex abscisus* (Riggenbach).

(3) *Corallobothrium* Fritsch 1886

With characters of family. Scolex with four suckers situated on the flat anterior face of the head. Many irregular folds and lappets of tissue about margin of anterior surface; may enclose suckers as in a corolla. No rostellum. No hooks nor spines. Neck broad, short. Habitat: In Siluridae.

Type species: *Corallobothrium solidum* Fritsch.

(4) *Crepidobothrium* Monticelli 1899

With characters of family. Head large, swollen, pyramidal, tetragonal, unarmed. Suckers large, inversely cordate, posterior margin interrupted and re-entrant into sucker cavity. Fifth sucker vestigial. Genital apertures marginal, irregularly alternating. Vaginal opening dorsal to cirrus pouch. Vagina anterior or posterior to cirrus-pouch. Testes in two lateral fields anterior to ovary. Habitat: In Boidae, South America.

Type species: *Crepidobothrium gerrardii* (Baird)

(5) *Acanthotaenia* von Linstow 1903

With characters of family. Scolex rather small. With four rounded suckers. Apex of head conical in which may be situated a vestigial fifth sucker. No rostellum. Cuticula of head and anterior part of body covered with minute spines or bristles. Segmentation indistinct. No overlapping of segments. Testes in two lateral fields anterior to ovary. Ovarian lobes may be branched. Vagina anterior or posterior to cirrus. Habitat: In Varanidae and Hylidae.

Type species: *Acanthotaenia shipleyi* von Linstow

(6) *Ophiotaenia* La Rue 1911

With characters of family. Head globose or somewhat tetragonal. No rostellum. No hooks or spines. Suckers circular or oval, with margins entire. Fifth sucker vestigial. Neck usually long. Testes in two long lateral fields anterior to ovary. Vagina anterior or posterior to cirrus-pouch. Ovary bilobed, flattened, sometimes alate. Parenchyma

with fine meshes. Musculature weak. Habitat: In aquatic snakes, Crotalinae, Colubridae, Elapinae and Amphibia.

Type species: *Ophiotaenia perspicua* La Rue 1911.

In the descriptive section the greater number of species of the above named genera have been described, with exception of species of *Acanthotaenia* and *Corallobothrium*. It has been impossible to write up the descriptions of certain species inquirendae of which no material could be obtained, and for which only very meager descriptions have ever been written. It is hoped that these may be properly considered at a later time.

## METHODS OF TECHNIQUE

The following methods have been used by the writer in the work on this group of cestodes. To a large extent they may be used with success on all groups of cestodes although it should be understood that certain methods which give admirable results with the relatively small and thin cestodes here dealt with will not give equally good results if used on the large forms such as *Taenia*.

The larger forms were picked out of the intestinal contents, care being taken to free the head if the worm was attached to the mucosa. These were then repeatedly dipped in the killing solution until the worm ceased to contract. The worm was allowed to lie for 15 minutes to 2 hours in the same fluid. Metallic instruments are to be avoided if corrosive sublimate solutions are used for fixation. When the smaller worms were encountered the whole intestine slit open was placed in a small quantity of physiological saline solution in a bottle which was then shaken vigorously for about 3 minutes, the killing fluid was added and the whole then shaken for one half minute. This is according to the method of Looss. The fixative was permitted to act 3 to 10 hours.

The killing fluids used were hot 5% solution of formaldehyde, and hot or cold saturated aqueous solution of corrosive sublimate to which was added glacial acetic acid to make 1 to 2%. Some other fluids were tried but nothing gave better results for the purposes of this study than the corrosive acetic mixture used hot or cold. For most of the worms the cold solution was preferable to the hot which sometimes gave rise to artifacts if used at too high a temperature. In no cases were the worms stupefied before killing.

The usual methods were used for hardening and dehydrating. Specimens were usually preserved in 85% alcohol after running up through

the grades. Sometimes after the corrosive acetic fixation 5% formalin was used for a preservative with uniformly excellent results.

Sections were cut 5 to 10 micra thick for the study of histological detail and 20 micra when grosser morphological details were sought. The sections were stained with haematoxylin mixtures, either Delafield's haematoxylin or Mayer's haemalum, and decolorized in the manner approved for these stains. Methods of staining in toto followed by sectioning were used with great success at times. For this purpose Ehrlich's acid haematoxylin much diluted with 50% alcohol gave the best results. For a contrast stain eosin in 95% alcohol was used on the sections. Acid fuchsin also in 95% alcohol was sometimes used effectively.

Preparations in toto were much used and were found to be of great value in mapping out the relationships of the organs of the proglottids. Frequently these methods showed everything to be desired except the histology of the organs. In some cases even histological details were well revealed by these methods. The stains which were tried for staining in toto were Mayer's paracarmine, Grenacher's borax carmine, some alcoholic cochineal mixtures, Mayer's haemalum, Delafield's haematoxylin, and Ehrlich's acid haematoxylin. None of the carmine or cochineal stains were very successful for none of them show the boundaries of cestode structures sharply. The parenchyma in which the genital organs lie always retained too great an amount of these stains to permit a clear view of the genital organs themselves. The haematoxylins, however, usually gave wonderfully clear, sharp pictures of the genital organs. It was at times possible to work out such minute structures as vasa efferentia almost in their entirety from such preparations in toto. The three haematoxylin stains were found to be about equally good.

In using these stains it was the practice to dilute the stain with the proper diluent. Relatively large quantities of the diluted stain were used for each lot of material. The stain was permitted to act over night (10 to 15 hours) at room temperature. The excess of the stain was then removed by washing in distilled water and the tissue passed through the grades of alcohol to 70% where it was decolorized rapidly by adding hydrochloric acid to make a 0.5 to 1.0% solution. The object was to remove the stain from the peripheral tissues at a rapid rate and meanwhile leave the stain in the deeper lying tissues. In this method the duration of the acid bath is usually short depending upon the size of the piece and the character of the stain taken by the tissue, and upon the character of the tissue itself. In general it is desirable to decolorize until a light reddish blue stain remains and until many of the internal structures can be distinguished while the tissue is still in the alcoholic medium. When in the judgment of the operator the proper stain is



attained the tissues are placed in neutral alcohol and then into 70% alcohol rendered slightly alkaline by the addition of a few drops of an aqueous solution of sodium carbonate.

Preparations were not flattened but were straightened out on a slide and over this was placed another slide which was supported by strips of paper of such a thickness that little or no pressure was exerted on the specimen by the slides. Dehydration and clearing were accomplished while the preparation was thus kept straight. Xylol and cedarwood oil were used as clearing agents. Preparations were mounted in balsam.

The methods outlined above yielded very satisfactory preparations for the study of these cestodes and they have also been used by the writer on other cestodes and on trematodes with great success. It is noteworthy that the carmine stains give beautiful preparations of trematodes in toto but fail almost entirely for cestodes. For the cestodes these stains fail because they do not sharply and clearly outline the sexual organs as they do in trematodes though not better than do the haematoxylin. In the judgment of the writer the use of the carmine stains on cestode material has been responsible for many errors in the interpretation of cestode structures.

## ANATOMY AND HISTOLOGY OF PROTEOCEPHALIDS

This section deals in a very general way with the anatomy and histology of the Proteocephalidae, placing emphasis on the usual character of the structures encountered and at times calling attention to variations in this general plan. In the descriptive part of the work the ordinary histological details and many of the anatomical details of lesser importance have been omitted or mentioned in only a casual way. Whenever the character of a structure has departed from the usual the fact has been noted in more or less detail.

The cestodes of the family are constructed on a uniform plan which has been thoroly discussed by Monticelli (1891), Kraemer (1892), Riggenbach (1896), Benedict (1900), Schneider (1905), Schwarz (1908), and La Rue (1909). Some new points are brought out in the present paper. The histological structures of these cestodes have been pretty well worked out prior to the present time. Von Linstow (1891), Monticelli (1891), Kraemer (1892), and Riggenbach (1896) did pioneer work on the histology of the group. Riggenbach (1896) and Benedict (1900) made very careful and accurate studies of the histology of certain species of fish Proteocephalids and were able to clear up some of the earlier misconceptions. No careful work on the histology of the amphibian

Proteocephalids was made until the work of the writer (La Rue, 1909) on *Ophiotaenia* (*Proteocephalus*) *filarioides*. Subsequent work on the histology of the cestodes of snakes has shown but little new, altho it must be admitted that only little has been done on the group.

The scolex is usually of small size and rather inconspicuous. Among the fish Proteocephalids the heads range in size from a little more than 0.1 mm. in breadth to about 1. mm., tho in at least one species, *P. sulcatus*, the breadth of this region attains as much as 1.75 mm. Among the amphibian and reptilian Proteocephalids the heads range from about 0.2 mm. to 1.75 mm. in breadth. In general the head is not sharply delimited from the neck, which may be of nearly equal width or in exceptional cases even wider for a short distance than the head. In form the heads show considerable variation. They are usually more or less globose or conical, and somewhat flattened dorsoventrally. In a few cases the head may present a more or less flattened tetragonal anterior face. The surface of the heads may be smooth or marked by shallow or deep grooves between the suckers. As a rule the heads have no folds or lappets of tissue about the suckers or on the anterior face. Such structures are found, however, in *Corallobothrium* and to a more limited extent in *Choanosclex*. The special characters of the heads of each species are taken up in the descriptive part of the work. The heads of Proteocephalidae and Monticellidae differ from those of other families of Tetraphyllidea in that the suckers are sessile, and have no accessory areola. Even when the head is deeply furrowed the sucker never has the appearance of having a stalk. Suckers may be prominent or inconspicuous and so may influence the general appearance of the head.

A rostellum is unknown among the species of this family, altho certain species have been erroneously reported to have such an organ. It is possible, tho not probable, that some species of *Acanthotaenia* have a rostellum. Some of these species have long apical prominences on the head, but except for the elongation of this apex and the presence of cuticular spines there is no evidence for considering this structure to be a rostellum. The spines are not hooks but are cuticular structures which may extend over the anterior part of the body. Neither elongated tip nor cuticular spines are good criteria of the presence of a rostellum. To determine the presence of a rostellum one should look to the inner structure of the apex, its musculature and protrusibility, and to the origin of this rostellum-like tip. In the tip of the heads of many species which do not possess a functional fifth sucker there has been found a peculiar structure consisting of massed cells and sometimes a few muscular elements. This structure has been considered to be a rudimentary

rostellum. Such a supposition, however, is incorrect, for in its development it is a fifth sucker. A more complete discussion of this rudimentary or vestigial fifth sucker is given under the proper caption (vide infra).

All species are provided with four suckers and some with an apical fifth sucker in addition. The latter may be either functional or vestigial. The four suckers are sessile, prominent, or inconspicuous cup-shaped organs which are usually situated on the broadest part of the head or just anterior to the broadest zone. In *Corallobothrium* the suckers are situated on the flattened anterior face of the head. The suckers do not possess accessory areola nor are they provided with hooks in their cavities or on their margins. *Acanthotaenia* may have cuticular spines within the sucker cavity. Suckers are usually rounded or oval in outline and may have deep cavities. The margin is usually entire but is at times interrupted. Some peculiar cases occur: *Proteocephalus cyclops* has suckers pointed at the posterior end. The suckers of *P. singularis* (Fig. 25) are flat, thin and weakly muscled and have a peculiar upturned point at the anterior margin. The deep grooves between the suckers of this species cause these organs to stand out prominently. *Crepidobothrium gerrardii* (Figs. 12, 13, 33, 34, 123, and 124) likewise has peculiar suckers in that each has an interrupted lower margin which forms a point re-entrant into the sucker cavity. Deep grooves between the suckers give the head a lobed appearance and cause the suckers to be prominent. *Proteocephalus osculatus* (Fig. 162) has a fifth sucker which is said to be covered with minute spinelets. The suckers of some of the *Acanthotaenia* are covered with minute spinelets. It is deemed unnecessary to enter into a discussion of the histology of the suckers of this group. Benedict (1900), Kraemer (1892), and La Rue (1909) have discussed this subject in detail.

A functional fifth sucker situated at the apex of the head is present in many species of *Proteocephalus* but is not known among the other genera of the family. Other species of *Proteocephalus*, *Ophiotaenia*, *Crepidobothrium*, and *Acanthotaenia* are known to possess a structure which the writer (1909) called an end-organ and which Johnston (1909 et seq.) has called an apical muscle-plug. Other species of *Proteocephalus* and all known species of *Corallobothrium* and *Choanoscolex* do not possess this structure or the functional fifth sucker while some species of *Proteocephalus* and *Ophiotaenia* have not been investigated for it. The writer has now determined that this organ is a vestigial fifth sucker. The fifth sucker when functional is usually smaller than the others and it possesses all the histological structures of other *Proteocephalid* suckers. The basement membrane and the muscles have the same relations as in other suckers.



The vestigial fifth sucker in the adult head is represented by a mass of cells or of nuclei and at times a few fibers surrounded by a basement membrane. It is entirely sunken into the tissues of the head and has lost all connection with the exterior. An examination of this structure in an adult head yields no clue to its probable origin, but if heads of plerocercoids of a species which has this structure in the adult be examined it is seen to be a degenerate fifth sucker. In the plerocercoid this degenerating fifth sucker has a sucker cavity communicating with the exterior. It has basement membranes and a full complement of muscles altho some of the muscles may be somewhat displaced and undergoing atrophy. The origin of this structure has been worked out in some detail for *Ophiotaenia filaroides* and the results are given in the description of that species. Its structure is illustrated by drawings which are reproduced here (Figs. 27, 28). The structure of the adult organ was given in the writer's paper on this cestode (La Rue 1909).

A vestigial fifth sucker which has not reached such a state of degeneracy as is found in many of the species occurs in the head of *Crepidobothrium gerrardii*. In this species the sucker tho so greatly reduced in size as to be overlooked in an examination of toto preparations still retains its cavity which is yet in connection with the exterior through a small pore. The sucker is surrounded by a basement membrane and it shows some traces of muscles altho the material studied was too poor to make a good histological study. A more complete description of this vestigial sucker is to be found in the description of *Crepidobothrium gerrardii*. Its structure is delineated in figure 42. In his description of these vestigial structures found in *O. filaroides* and in *C. gerrardii* the writer has conclusively shown that the organ under discussion is a vestigial fifth sucker and not a vestigial or rudimentary rostellum. It seems highly probable that similar structures found in other species of the group will prove to be vestigial fifth suckers.

The writer can see no reason for assuming that this structure is a rudimentary rostellum. So far as known a well developed rostellum does not occur among the Tetracophyllidea but is characteristic of many species of Cyclophyllidea. Unless an apical sucker is a transitional stage in the development (phylogenetic) of a rostellum the writer sees no reason for regarding this vestigial fifth sucker as a rudimentary rostellum. The knowledge concerning this structure is incomplete and studies of developmental stages of Proteocephalid species possessing vestigial or functional fifth suckers should be made in comparison with similar developmental stages of species of Calliobothrium and Anthocephalus which according to Lang (1881) and Monticelli (1888) have certain rudimentary structures that seem to be like the oral suckers of trema-

todes. Likewise a study should be made of certain species of Cyclophylidae which are known to possess a rudimentary or a vestigial rostellum. No definite solution of this problem can be reached without such a comparative study. Data as to the presence or absence of the fifth sucker in species of the group, whether functional or vestigial, is to be found in the tables of the principal characters of the cestodes of this family.

The nervous system is made up of a nerve ring which occurs in the neighborhood of the suckers and one pair of main lateral nerve trunks in the strobila. As described by the writer (1909) for *Ophiotaenia filaroides* the nerve ring is somewhat octagonal in shape and at its corners nerve processes extend out to the suckers. From the ring main trunks extend back into the strobila. In the strobila a single pair of main lateral trunks may be seen just within the lateral fields of the muscle sheath. No accessory nerve trunks have been made out by the writer. In *Ophiotaenia filaroides* the nerve trunk passes dorsal to the cirrus and the vagina.

In all species the neck is a more or less poorly defined unsegmented region between the head and the segmented part of the strobila. This region may be several millimeters long in certain species while in others it is said to be entirely lacking or may be no more than 0.3 to 0.5 mm. long. It is usually narrower than the scolex tho in exceptional cases in which the neck muscles may be unduly contracted the neck is broader than the scolex. Much confusion has arisen over the statements of the older investigators who described the neck of certain species as being long or very long without, however, giving measurements. These adjectives are relative terms. If the cestode is small, 0.5 to 1 mm. broad and 20 to 100 mm. in length, a neck which is 1 to 5 mm. long seems long or very long. A neck of that length on a cestode as large as *Crepidobothrium gerrardii* which is several millimeters broad and many centimeters long would be called short. In this species an unsegmented region 0.5-1 mm. long is ignored by some authors and the specimen is reported as having no neck. It is essential that actual measurements of the unsegmented region be made. For this purpose stained specimens are necessary because unstained specimens will not show segmentation plainly and also because external wrinkles or folds may simulate segmentation. In recording measurements of the neck the writer takes the length from the point of narrowing behind the suckers to the first evident traces of internal segmentation. In a few species another system has been found necessary but in these cases the method of measuring has been stated. The breadth given is the narrowest place in the unsegmented region.

The segmented part of Proteocephalids varies greatly in length, breadth, and thickness. In some species the strobila is small, being not

more than a few millimeters long and less than 1 mm. broad, while in others it may attain a length of 60 or more centimeters and an extreme breadth of 2 to 4 mm. Such extreme size is infrequent even for the large species. Many of the species of *Proteocephalus* are thick and fleshy while a few of them are thin and flat. So also are the known species of the family *Monticellidae*. Segmentation may be evident or obscure. Perhaps in no species is it as evident as it is in some species of *Taenia*. The proglottids are usually without sharp posterior angles and they are attached along their entire width. Transverse intersegmental furrows if present are shallow.

The youngest proglottids are very indistinct and are distinguished in stained preparations as faint cross bands of alternate dark and light. These are darkly stained areas of rapidly differentiating parenchyma alternating with the unstained future septa. Almost without exception the young proglottids are much broader than long. The reverse of this is true only when the anterior part of the body is in an extremely attenuated condition. As the young proglottids develop they increase in length and breadth, tho the length usually increases more rapidly than the breadth. The transition from young to mature proglottids is gradual. Mature proglottids are those in which the sexual organs have attained maturity and egg production is about to begin or may just have begun. Such proglottids are usually broader than long or quadrate. The length is much greater than in the young proglottids. Mature proglottids are the best ones in which to study the greater part of the genital system tho of course a study of the uterus must be made from the ripe proglottids.

Those proglottids in which egg production is well along or complete are spoken of as ripe proglottids. The uterine pouches are full of eggs and the ventral openings are preparing for their discharge. Ripe proglottids are frequently longer than broad tho the reverse is not uncommon. They are normally considerably larger than mature proglottids. In them the vitellaria and testes may be greatly reduced in size or almost obliterated by the great mass of eggs in the uterine pouches. An end-proglottid is frequently present. This should be defined as the first proglottid to be differentiated from the growing zone of the neck. It still retains certain of the characters of the posterior end of the plerocercus which is not lost in the passage of the young tapeworm through the stomach of the host. It is pointed posteriorly and has at the tip a median excretory pore through which the excretory products are discharged. Just anterior to this pore, in some species, is a contractile bladder. In the species examined by the writer a number of end-proglottids have been found; some of these contained eggs and so are to be



considered as functional. Since ripe proglottids are shed after or about the time that the eggs are ripe one frequently encounters strobilas which lack the end proglottid. The loss of this proglottid is not to be considered as a special character, for it is common to many cestodes outside the group.

Two pairs, dorsal and ventral, of main lateral excretory trunks extend through the strobila. Of these the ventral vessels are the larger. Some additional longitudinal vessels have been described by von Linstow (1891) in *Proteocephalus longicollis*. It seems probable that he saw the cut ends of branches and anastomoses. Some species have a commissural vessel connecting the ventral excretory vessels at the posterior end of the proglottid. It has not been noted in other species. In the neck region and throughout the strobila many small branches arise from the ventral vessels and some also from the dorsal vessels which pass to the surface of the worm where they discharge to the exterior through a small pore. These openings occur more frequently on the ventral surface but may be found on the lateral edges. In most species they are irregularly distributed but in *Corallobothrium lobosum* Riggensbach (1896) found that they regularly came to the exterior at the posterior corner of the proglottid. This finding has not been supported by subsequent work on other species. In the head and the anterior neck region there are numerous coils of vessels and anastomosing branches of the same which extend well into the tip of the head. These coils lead back and are connected with the main lateral excretory trunks. At the posterior end of the worm the excretory vessels discharge, if the end-proglottid is present, through a common excretory pore (Fig. 51). Just anterior to this pore and discharging through it is sometimes a pulsatile bladder which is most readily seen in the plerocercus. The flame cells at the ends of minute vessels which discharge into the main vessels or into the larger branches are situated in the medullary parenchyma not far from the main excretory vessels. They have not been found in the cortical parenchyma nor in the mid-field of the proglottid. Their distribution in *Ophiotaenia flaroides* and *Proteocephalus ambloplitis* has been thoroly worked out (La Rue 1909).

The cuticula and the subcuticular structures are scarcely worthy of discussion here for in details of structure they do not differ from other cestodes. In the *Acanthotaenia* alone are there special features of the cuticula to which attention should be called. Here the cuticula is thrown up into minute cuticular spines which are too minute to be called hooks or hooklets. This condition is most prominent on the head and neck but may also occur to a smaller extent over the cuticula of the entire body. These features have been emphasized by von Linstow (1903) and John-

ston (1909, 1911, 1912a). Outside of this genus the only other species to have cuticular hooklets or spines is *Proteocephalus osculatus*, in which they are reported to have been found on the apical fifth sucker.

The parenchyma resembles that of other cestodes but is more loose than in the Cyclophyllidean cestodes which the author has examined. In the parenchyma the cell outlines are indistinguishable but there are numerous structures present which look somewhat like minute fibrillae. Large fat spaces are usually visible in the prepared sections and sometimes in toto preparations. In *O. filaroides* studied by the author (1909) the fat spaces are spheroidal or ovoidal in form and have a dimension of 0.03 to 0.045 mm. Similar spaces have been observed in other species of the family. They are smaller in the fish cestodes studied and larger in the snake and amphibian cestodes. The fat of fresh cestodes or of those recently killed in formol is readily stained by osmic acid solutions or by an alcoholic solution of Sudan III. Other specific fat stains have not been tried. The character of the parenchyma affects the staining properties of the cestodes. Those cestodes having a loose parenchyma make much better toto preparations than do those which have the dense parenchyma.

In general the parenchyma of the group of snake Proteocephalids is a more open, looser network than that of the fish Proteocephalids. There is more of the fibrillar structure present in the parenchyma of the latter than of the former. Whether this character is correlated with differences in environmental stimuli is not known. Perhaps the appearances of the parenchyma of cestodes can be explained as are the appearances of the connective tissues of higher animals. If this be true then it is evident that the closer woven texture of the parenchyma in fish cestodes is indicative of more frequent stresses and strains placed upon the cestode by the activity of the host or by the movement of ingested materials through the alimentary tract.

The sub-cuticular muscles resemble those of other cestodes. The circular and longitudinal fibers are not strong. Within the layer of sub-cuticular cells of the strobila there is a layer of longitudinal muscle fibers which separates the cortical from the medullary parenchyma in which lie almost the entire generative organs. This layer of fibers forms what is known as the inner muscle sheath. The sheath is well developed in some species, particularly in the larger species of fish Proteocephalids, while in the weaker species and in *Ophiotaenia* especially it is poorly developed. In these cases the muscles are few in number and separated from each other by intervals. The muscles of the inner sheath pass through the intersegmental septa. Other muscle fibers which pass through the tissues of the proglottid from dorsal to ventral and from

the lateral edges are frequently encountered but are not as numerous as are the fibers of the muscle sheath; they do not occur in groups but usually singly. In the region of the septa the transverse and dorso-ventral fibers are more numerous and form a sort of muscular plate.

The muscles of the head are not arranged in the same order as in the Cyclophyllidea, as La Rue (1909) pointed out. In transverse sections of the head the muscles are usually encountered as follows: Near the tip is a rhomboid of muscles, deeper down a transverse muscle cross and then a diagonal muscle cross, the last two forming a muscle star. The muscle star occurs in the region of the suckers but in certain cases (Riggenbach 1896) it may extend below the level of the suckers. Usually as soon as the suckers have been passed the muscles take on an arrangement typical of the muscle arrangement in the neck and the young proglottids. In longitudinal sections certain heavy muscle fibers are seen to pass from the neck to the surface of the head near the tip, others (the greater number) pass in bundles to the lower and inner surfaces of the suckers. A vertical muscle cross connecting the two adjacent suckers by the lower margin of each sucker to the upper margin of the other is also distinguishable. The muscles of the head have not been studied in many of the species. The writer has studied them in *Ophiotaenia filaroides*, *Proteocephalus ambloplitis*, and *P. singularis* and to a certain extent in *P. pinguis*. The muscles of the head of *P. singularis* are described in another part of this work (vide infra) with drawings illustrating the structures found. Riggenbach (1896) has studied the musculature of the head of *P. fossatus* and *Corallobothrium lobosum*. In the latter he noted certain variations from the type found in other Proteocephalids. These variations are associated with the type of head found in that genus.

The genital pore is situated on the lateral margin of the proglottid, right or left. Its position alternates irregularly from one side to the other. For each species the genital pore has a fairly constant location on the margin. In some species it is near the middle, and in other cases it is posterior to the middle, in others anterior. A genital papilla or eminence on which the pore is situated is not usually present. In one species, *Ophiotaenia grandis*, there is frequently a marked pitting or contraction about the genital pore which causes the latter to be deeply set back from the straight line of the margin. The genital pore leads into the genital atrium into which typically both cirrus and vagina open and to which the outer end of the cirrus-pouch is attached. The atrium is to be considered as an invagination of the outer body wall of the proglottid.



The cirrus-pouch, cirrus, ductus ejaculatorius, vas deferens, vasa efferentia, and testes comprise the male reproductive system.

The cirrus-pouch is a more or less cylindrical or ovoidal muscular bag which contains the cirrus and ductus ejaculatorius. At its outer end it is attached to the wall of the genital atrium by means of some of its muscle fibers. At the other end strong muscle fibers attach it to the inner dorsal surface of the muscle sheath. Some muscles are also continued into the cirrus itself. The form and size of the cirrus-pouch is reasonably constant for each species if proglottids of the same degree of development be considered. Hence the length of cirrus-pouch relative to the breadth of the proglottid is useful as a diagnostic character. In some instances the cirrus-pouch is somewhat constricted about the middle. This condition seems to be correlated with the act of protrusion, as the writer points out under a later caption. The greatest diameter is usually found at the inner end of the pouch.

The more or less muscular cirrus, a tube the two ends of which vary somewhat in structure, passes through the length of the cirrus-pouch. The outer portion of the tube is called the cirrus while the inner and less muscular end is called the ductus ejaculatorius. Each part is characterized by certain structures tho the one grades over into the other almost imperceptibly. The cirrus possesses both circular and longitudinal muscles. The circular muscles are most heavily developed near the base or outer end of the cirrus while they are greatly reduced in the end where it passes over into the ductus ejaculatorius. Longitudinal muscles are weakly developed. At the outer end strands of muscle pass out from the cirrus to the wall of the cirrus-pouch. There are very few if any gland cells on its exterior. Its internal surface is lined by a continuation of the cuticula of the atrium. Toward the inner end of the cirrus the cuticula gradually disappears until at the inner end it is difficult to distinguish. The muscles also become weaker and the outer diameter of the tube may consequently diminish in size tho in some species this region may be inflated. With the change in the musculature and the thinning of the cuticular lining prostate gland cells appear. These characters mark the ductus ejaculatorius, namely, the thin wall, weak muscles, little or no cuticula, and the presence of the prostate gland cells. This region may be swollen into a voluminous tube for the retention of spermatozoa and hence with the coils of vas deferens may serve as a vesicula seminalis. There is no specialized vesicula. The cirrus itself is usually quite straight and is only rarely thrown into coils. The ductus ejaculatorius is frequently straight tho in a large proportion of the species it is bent or coiled in one to several coils.

Since the outer end of the cirrus tube is fastened to the mouth of the cirrus-pouch the cirrus is everted when protrusion takes place. The protruded cirrus is then of double thickness, being made up of the heavier walled outer tube and the thin walled inner tube. In certain species of *Ophiotaenia*, viz., *O. marenzelleri* and *O. trimeresuri*, one to three or more coils of ductus ejaculatorius are forced out into the swollen base of the cirrus. This could only occur in species in which the ductus has a considerable length. Species having a short straight ductus would not show this character. In the cases above cited the cirrus-pouch is not evaginated as Schwarz (1908) stated was true of *O. marenzelleri*. This condition of the cirrus and ductus is more fully discussed under the descriptions of *O. marenzelleri* and *O. trimeresuri*. (See also Figs. 106, 108, 199.) Such a pushing out of coils of ductus into the cirrus is not known among the species of *Proteocephalus*, *Choanotaenia*, *Crepidobothrium*, or *Monticellia*. The writer has recently seen it in some proglottids of a species of *Ophiotaenia* from a king snake from Florida.

In certain species, notably *P. fallax* (Fig. 57) a set of strong circular muscles and a constricted area may be found about the middle of the cirrus-pouch. The inner end of the pouch may also be swollen. The presence of these muscles together with the constricted area which is not usually seen and the swollen inner end suggest a possible explanation of the process of cirrus protrusion. In all species the circular muscles of the sheath or pouch are fairly well developed while the longitudinal muscle fibers have a weaker development. A contraction of the circular muscles and perhaps also of longitudinal muscles would produce a relatively high pressure upon the contents of the cirrus-pouch. The inner end of the pouch is closed, the outer end is opened broadly and at the edges of this broad opening the cirrus walls are attached. It is evident therefore that the only escape for the contents which are under pressure is by means of this open end of the pouch through which the cirrus is everted. As an aid in the beginning of the act of protrusion, relaxation of the muscles of the cirrus and a contraction of the weak muscles which connect the cirrus to the cirrus-pouch may play a part. This action once initiated the hydraulic pressure put upon the contents of the cirrus-pouch by the contraction of the muscles of the pouch would complete the act of eversion. In certain cases where the cirrus and the ductus ejaculatorius form a straight tube through the cirrus-pouch it seems probable that a shortening of the pouch is also necessary. Such a shortening has not actually been observed.

The retraction of the cirrus is not so easily explained. It seems that strong contractions of the longitudinal muscle fibers within the walls of the cirrus and ductus ejaculatorius would be of great assistance in

retraction. In many species the muscle fibers connecting the cirrus with the walls of the cirrus-pouch seem entirely too weak to assist much in this process. Since the inner end of the cirrus-pouch is attached to the body wall by strong muscles their contraction would lengthen the cirrus-pouch and this would exert a direct traction upon the ductus ejaculatorius. Such a lengthening of the pouch would tend toward the production of a negative pressure which might draw the cirrus back into the pouch. In some species large numbers of cirri have been seen protruded, in others none or almost none. Protruded and unprotruded cirri have been noted among both mature and ripe proglottids. These facts stimulate one to inquire whether the cirri are normally retracted after protrusion? Is protrusion of the cirrus a common occurrence in the act of copulation or is it an accident? Had those unprotruded cirri in the ripe proglottids ever been protruded? These are questions that cannot be answered from the available data nor has the author seen anything in the literature on these points. An opportunity is suggested here for experimental work.

Riggenbach (1896) considered that the broad cavity of the cirrus might be called a vesicula seminalis and that this cavity functioned as such an organ. While it is true that the cavity of the cirrus and ductus ejaculatorius might function as a vesicula, they are not structurally a vesicula. When the sexual organs become fully mature the semen is stored until ejaculated in the coils of the vas deferens which become greatly swollen. Thus the coils of vas deferens function as a vesicula seminalis altho they are not differentiated into such an organ. Properly speaking there is no vesicula seminalis in the Proteocephalidae. The vasa efferentia and vas deferens have been carefully described by Riggenbach (1896) and La Rue (1909). Altho they have been observed in a number of species of the family they have not been especially re-described in the descriptions of the species because they are essentially the same in all species of the group. Their general relations may be seen in figures 90 and 180. The vasa efferentia are thin walled small tubes leading out from the covering of the testes. These tubules anastomose with some of their neighbors and finally the larger vessels unite with the inner end of the vas deferens. The vasa efferentia can sometimes be studied from toto preparations of proglottids if the testes were discharging semen at the time of killing the cestode. Carefully made frontal sections stained with haematoxylin sometimes show them very well. The vas deferens is a thin walled tube of larger diameter than the vasa efferentia. It begins near the middle of the proglottid on the inner dorsal surface of the muscle sheath. Then it makes a few or numerous coils which extend to the inner end of the cirrus-pouch which it enters. From



this point the vas deferens is continuous with the ductus ejaculatorius and the cirrus.

Testes are numerous small ovoidal or spheroidal bodies which lie toward the dorsal surface of the medullary parenchyma within the longitudinal muscle sheath. They occupy as a rule nearly the entire space between the lateral vitellaria anterior to the ovary. They leave a small free area in the region of the coils of the vas deferens. In the genus *Proteocephalus* the testes form one or two layers which extend from one vitelline field to the other. In one species, *P. torulosus*, they extend past the ovary to the posterior margin of the proglottid. In the genus *Corallobothrium* the testes form a single broad field anterior to the ovary. In *Ophiotaenia*, *Crepidobothrium*, and *Acanthotaenia* they form two lateral fields, one on either side of a free median zone. In rare cases some scattered testes may be found in this median zone. In these genera, which have been but little studied by the section method, the testes seem to form a single layer in depth. The number of testes varies widely from about 25 in some to about 400, the upper limit for other species. For each species there seems to be a characteristic number which is not constant but varies within certain limits. This range is usually not great, being 5-10-15 for cestodes with the smaller number of testes and very much greater for those cestodes which have very numerous testes. *Crepidobothrium gerrardii* has from about 200 to 400 testes, the range being about 200. In mature proglottids the testes are most plainly seen. As the uteri develop and the eggs fill the uterine pouches the testes are pushed aside by the swollen uteri or they shrink and are lost to view between the walls of the uterine pouches.

The organs which comprise the female reproductive system are vitellaria, vitelline ducts, vagina in all its parts, ovary, oöcapt, oviduct, oötype, shell glands, receptaculum seminis, uterine passage and uterus. The vitelline follicles are small spheroidal bodies which are arranged in two long bands which extend the full length of the proglottid near the lateral margin of the latter. The follicles usually are rather compactly grouped about the central conducting tubule. Rarely the vitellaria extend past the posterior edge of the ovarian lobes, and in only one known case, (*Proteocephalus perplexus*), do they follow along the posterior margin of the proglottid (Figs. 54, 55). The vitellaria are inside the longitudinal muscle sheath and very near the lateral nerve trunks. The central conducting tubules near the posterior end of the proglottid are known as the paired vitelline ducts which lead to the middle of the proglottid where they unite to form the common or unpaired vitelline duct. This may dilate to form a vitelline receptacle. From the vitelline receptacle the unpaired duct passes backward to join the oviduct just before

the latter enters the oötype. The course of these ducts as described by von Linstow (1891) and Kraemer (1892) was incorrect. Riggenbach (1896) and Bendict (1900) established their true course. The vitelline ducts, paired and unpaired, are made up of thin tissue possessing no glandular elements.

The vagina is a tube of varying dimensions and character leading from the genital atrium to the middle of the proglottid and thence posteriorly to the interovarial space where it unites with the oviduct to form the fertilization canal, which is a part of the oviduct. The vagina and cirrus-pouch alike open into the genital atrium. The initial part of the vagina may lie anterior or posterior to the cirrus-pouch and the opening of the vagina may have either of these positions, but in some species examined especially for this point the opening was dorsal to the cirrus-pouch. In *Proteocephalus* the vagina is usually anterior to the cirrus-pouch altho there are a few species in which it is regularly posterior. In species of *Ophiotaenia* it is as frequently posterior as anterior to the cirrus-pouch, but in *O. filaroides* alone it has never been observed in the posterior position. In *Acanthotaenia* and *Crepidobothrium* the vagina may be either anterior or posterior. The vagina on account of its varying structure may be subdivided into four parts. These are (1) the initial part reaching from the genital atrium nearly to the middle of the proglottid, (2) the tube extending back to the interovarial space where its structure changes to (3) the receptaculum, and then (4) the lower vagina extending from the receptaculum seminis to the oviduct. These parts are distinguished by position and by structure. The initial part has an opening into the genital atrium. It is lined usually by a cuticula which in some species may be traced almost back to the receptaculum. The initial part is frequently somewhat broadened out and is somewhat muscular. Near the opening to the atrium the muscles are usually developed into a sphincter muscle, the sphincter vaginae. This may have a strong development (Figs. 106, 183) or may be very weak (Figs. 47, 50, 57). The modifications of the sphincter serve as distinguishing characters. Noticeable on the initial part of the vagina particularly but also occurring on almost the entire length of the vagina are numerous gland cells.

The longitudinal tube of the vagina presents some different appearances from the initial part. It is usually a straight or wavy thin walled tube of large or small diameter depending on the species and the stage of development of the proglottid. In some species as the proglottid becomes mature or especially after coitus this part of the tube is much dilated. In all species the musculature of this part of the tube is very weak or lacking entirely. Here also the cuticula of the initial part of

the vagina may disappear or is very thin and difficult to determine. In *Proteocephalus macrocephalus* and a few other species the vagina is ciliated throughout almost its entire length. Just after the long tube of the vagina enters the interovarial space or in some species just anterior to the mid-piece of the ovary the vagina broadens out slightly and this is followed by a sudden diminution in diameter and a change in the histological structure of the tube. This broadened part is known as the receptaculum seminis, the presence of which Riggenbach (1896) denied. Since it is somewhat different histologically and also since it serves the function of a receptaculum it may well be called a receptaculum. The writer has already presented his views on this matter in his description of the organ in *Ophiotaenia filaroides* (La Rue 1909). Since that time he has observed the structure in several other species and sees no reason for changing his view. From the receptaculum seminis to its junction with the oviduct the vagina may be spoken of as the lower vagina. This part is characterized by its small diameter, thick muscular walls and rich investment of gland cells. It is not ciliated in any part of its course in any species studied by the writer. The lower vagina frequently describes a long loop or several coils within the interovarial space.

The ovary as in other Tetraphyllideans is situated in the posterior end of the proglottid, is bilobed and the lobes are connected by a mid-piece. The lobes are thin, alate or club-shaped, branched or made up of several slender blind pouches, or the branches may anastomose. Rarely or never is the lobe a solid mass but it seems to be made up of more or less anastomosing branches or tubes. The whole ovary is closely invested with a thin membrane. The organs of the interovarial region are taken up as nearly as possible in the order of occurrence, beginning with the oöcapt. The general relations of these structures are shown in drawings which have been reproduced (Figs. 99, 104). The oöcapt is a funnel-shaped muscular organ attached to the mid-piece of the ovary and present in all the species examined. It is made up of circular and longitudinal muscle fibers and is surrounded by scattered gland cells. In action it is a gulping organ which by its rhythmic contractions forces the ova down the oviduct. The oviduct is a thick-walled tube made up of epithelial cells and around these are circular and longitudinal muscle fibers. Some gland cells are scattered along its entire length and it is lined with numerous long cilia. In its course from the oöcapt it describes one or more loops or coils and then it receives the lower vagina which here pours the sperms upon the ova. The oviduct from this point on should be known as a fertilization passage. This passage, which is relatively short, discharges into the oötype. However, just before entering into the oötype the oviduct receives the unpaired vitelline duct which pours out



the product of the vitelline glands. The oötype is a slightly elongated muscular organ of small size. Its muscles are much heavier than those of the oviduct and they represent, perhaps, a higher development of the oviductal muscles. About the oötype is found a large number of long slender cells which in the aggregate have been called the shell-gland. Each cell evidently discharges by its own minute duct which may be traced well down between the muscles of the oötype. In the oötype the egg is formed. The oötype discharges directly into a duct called the uterine passage. This duct leads forward directly or after a few coils have been described and discharges the formed eggs into the median stem of the uterus at a point which is usually anterior to the posterior end of the uterus and on the dorsal side of the latter. In structure the uterine passage differs from the oviduct in the lack of strong musculature. Sometimes it is difficult to find any musculature at all. There are scattered gland cells and numerous nuclei of cells which are of an epithelial nature or which belong to cells of parenchymatous origin. These structures of the interovarial space have been worked out by Monticelli (1891), von Linstow (1891), who made numerous errors; by Kraemer (1892), who likewise made some errors. Riggensbach (1896) did very careful work and so also did Benedict (1900), altho the latter erred in denying the existence of a uterine passage for his species. More recently the writer (La Rue 1909) has worked out all these points in considerable detail.

In all the species of the family the uterus develops as a median longitudinal tube (Fig. 105) lying in the medullary parenchyma just within the longitudinal muscle sheath and toward the ventral side of the proglottid, while the testes occupy the field toward the dorsal side of the proglottid. This long tube extends almost from the anterior end to the mid-piece of the ovary. The stem of the uterus is first seen as a rod of deeply staining cells which seem to arise from differentiating parenchyma cells in young proglottids. The rod after a considerable multiplication of cells becomes hollow throughout its entire length. By the method of outpocketing described by La Rue (1909) the uterus sends out a few or numerous branches to the right and left. These branches begin as rods of cells which rapidly multiply. Then a cavity opens through the length of the rod somewhat as the lumen appears in smaller blood vessels during the development of higher animals. The rod continues to increase in length and the lumen to extend as the rod lengthens. A few of the outpocketings are directed ventrally and these eventually pierce the ventral body wall (Fig. 89) and thus provide opportunity for the discharge of eggs. The lateral pouches are formed prior to the discharge of eggs into the uterus and in all cases observed the pouches increased in size so rapidly that there was no crowding of eggs until the

uterus had almost attained its complete development. Those workers who ascribe the production of these pouches to the crowding of the eggs have evidently failed to read the evidence to be seen in the developing uterus. Likewise those who ascribe the splitting of the proglottid down the ventral side to the pressure of contained eggs have failed to note the fact that the ventral pouches perforate the ventral side in one or more places before the pressure of eggs is great enough to split the proglottid.

The number of pouches on either side varies greatly but is reasonably constant for each species. *Proteoccephalus longicollis* with its three pouches (Fig. 167) on either side has the smallest number, while some of the *Ophiotaeniae* (Fig. 101) have as many as thirty or more. When filled with eggs the pouches in many species fill almost the entire ventral field of the proglottid, while in some species of *Ophiotaenia* they apparently take up but little more than half the width of the proglottid. The pouches come to lie very close together, so that only small septa separate them. Testes are pushed laterally or nearly obliterated by the pressure of filled pouches. The vitellaria likewise are nearly obliterated in many species while the ovarian lobes usually shrink considerably at this time. The splitting of the ventral surface and the discharge of the eggs occurs soon after. The wall of the uterus in its early stage of development appears to be made of an epithelium the cell boundaries of which are indistinct or invisible, altho the nuclei are very prominent and are closely packed together. In the later stages of the uterus the nuclei are farther separated, the outlines of the cells cannot be seen at all even tho the membrane in which the nuclei lie is thick and apparently tough. Riegenbach (1896:92) says, "Eine dicke Membran bildet die Wand des ganzen Fruchthalters. Nach aussen lagern derselben stets viele kleine Zellen auf, die zwar kein eigentliches Epithel bilden, wie es bei andern Cestoden oft der Fall ist, jedoch als Reste eines solchen anzusehen sind." In this view Riegenbach may be correct.

The eggs usually have three membranes altho in a few species the eggs have been recorded as having two membranes. In these cases it is possible that a third membrane was overlooked. The outer membrane of eggs that have been discharged into water is usually much larger than the others. It is thin, hyaline and spheroidal in form. Eggs preserved in utero and later examined do not show this membrane at all prominently and in some cases it might easily be considered as a part of the second membrane. The outermost membrane is smooth in outline. The only known exception is found in the eggs of *Ophiotaenia nattereri* which Schwarz (1908) described as having peculiar branched hooklets about its periphery. His drawing of this egg is reproduced (Fig. 194). The middle membrane is usually thick and granular and

but little larger than the embryo. The third or inner membrane is a delicate but tough and clear membrane which is not always easy to demonstrate. It is closely applied to the embryo and might readily be overlooked.

#### CHARACTERS OF DIAGNOSTIC VALUE

Benedict (1900:339) in his discussion of these forms called attention to the small dependence that can be placed upon external measurements when used alone as a means of determining species. While in the main he is correct in his contentions it is certainly a fact that such measurements when used in conjunction with other data may be of great value and these should always form a part of the species description. These measurements should include the dimensions of the head and suckers, the length of the strobila and its breadth at intervals or the breadth of proglottids at certain stages of development. The dimensions of proglottids are always of service, and of less importance are the dimensions of the neck. Data as regards the host, the locality and the habitat of the host are always of value. The older investigators made much of these data and justly so for they were unable to make a study of the internal anatomy of cestodes. At the present time such data do not seem to be as highly valued as they should. The anatomy and finer structure of the internal organs furnish the most valuable characters for diagnostic purposes. The relations of the external genitalia, of the male and female reproductive organs to each other, the number and size and distribution of the testes, character of the coils of the vas deferens, size and character of the cirrus-pouch, cirrus, ductus ejaculatorius, and the protruded cirrus are all of value for diagnosis. So also are the relations of the various parts of the vagina, the vitellaria, ovary, oviducts and all of the small organs of the interovarial space. Of especial value are data in regard to the pouches of the uterus and the measurements of the egg membranes and the embryo. The presence of muscular elements and cilia may at times be used as distinguishing features. Drawings showing the essentials of external and internal anatomy should always form a part of a report on these animals.



# KEY TO THE BETTER KNOWN GENERA AND SPECIES OF PROTEOCEPHALIDAE

- 1(70) Proteocephalids with heads which have no folds or lappets  
of tissue about the suckers..... 2
- 2(47) Testes lie in a single broad field between vitellaria; para-  
sitic in freshwater fish.  
Genus *Proteocephalus* Weinland 1858..... 3
- 3(24) Functional fifth sucker lacking, i. e. absent or vestigial..... 4
- 4(15) Testes number 100 or more..... 5
- 5( 8) Cirrus-pouch extends  $\frac{1}{3}$ - $\frac{1}{2}$  across breadth of proglottid..... 6
- 6( 7) Uterine pouches 4 to 8 on either side; ductus ejaculatorius  
nearly straight.....*Proteocephalus agonis* (Barbieri 1909)
- 7( 6) Many uterine pouches on either side; ductus ejaculatorius  
forming several coils.  
*Proteocephalus fossatus* (Riggenbach 1896)
- 8( 5) Cirrus-pouch extends less than  $\frac{1}{3}$  across the breadth of the  
proglottid ..... 9
- 9(12) Genital pore situated at middle of lateral margin of proglot-  
tid ..... 10
- 10(11) Uterine pouches 3 to 4 on either side; testes in 2 layers; cir-  
rus-pouch extending  $\frac{1}{4}$ - $\frac{1}{6}$  across the breadth of the  
proglottid; suckers 0.18-0.2 mm. in diameter.  
*Proteocephalus torulosus* (Batsch 1786)
- 11(10) Uterine pouches 7 to 14 on either side; testes in 1 layer, cir-  
rus-pouch extending  $\frac{1}{6}$ - $\frac{1}{8}$  across the breadth of the  
proglottid; suckers 0.095-0.16 mm. in diameter.  
*Proteocephalus macrocephalus* (Creplin 1825)
- 12( 9) Genital pore anterior to middle of lateral margin of pro-  
glottid ..... 13
- 13(14) Uterine pouches 20 to 25 on either side; vagina anterior to  
cirrus-pouch; 135-155 testes.  
*Proteocephalus perplexus* La Rue 1911
- 14(13) Uterine pouches 10 to 12 on either side; vagina posterior to  
cirrus-pouch; about 200 testes.  
*Proteocephalus sulcatus* (Klaptocz 1906)
- 15( 4) Testes number less than 100..... 16
- 16(17) Suckers with pointed apex and shallow cavity.  
*Proteocephalus singularis* La Rue 1911
- 17(16) Suckers round or oval with smooth contour..... 18

- 18(19) Vaginal sphincter very long and strong; cestode large, robust.....*Proteocephalus ambloplitis* (Leidy 1887)
- 19(18) Vaginal sphincter short and weak; cestodes small..... 20
- 20(23) Testes in 2 partial or complete layers..... 21
- 21(22) Cirrus-pouch extends  $\frac{1}{3}$ - $\frac{1}{4}$  across the breadth of the proglottid; ductus ejaculatorius forms several coils; 75-90 testes.....*Proteocephalus filicollis* (Rudolphi 1802)
- 22(21) Cirrus-pouch extends about  $\frac{1}{2}$  across the breadth of the proglottid; ductus ejaculatorius nearly straight; 44-52 testes.....*Proteocephalus esocis* (Schneider 1905)
- 23(20) Testes in one layer.....*Proteocephalus neglectus* La Rue 1911
- 24( 3) Functional (well developed) fifth sucker present..... 25
- 25(26) Suckers pointed at posterior margin.  
*Proteocephalus cyclops* (von Linstow 1877) sp. inq.
- 26(25) Suckers not pointed at posterior margin..... 27
- 27(42) Testes number about 70 or less..... 28
- 28(35) Cirrus-pouch extends less than  $\frac{1}{3}$  across breadth of proglottid ..... 29
- 29(32) Embryos 0.03 mm. in diameter or greater..... 30
- 30(31) Uterine pouches 6 to 8 on either side; 30-35 testes situated in 1 layer.....*Proteocephalus fallax* La Rue 1911
- 31(30) Uterine pouches 7 to 14 on either side; 55-60 testes situated in 2 partial layers.....*Proteocephalus dubius* La Rue 1911
- 32(29) Embryos much less than 0.03 mm. in diameter..... 33
- 33(34) Uterine pouches 9 to 14 on either side; 35-40 testes; cestodes very small.....*Proteocephalus exiguus* La Rue 1911
- 34(33) Uterine pouches 4 to 9 on either side; 50-60 testes; cestodes of medium size.....*Proteocephalus percae* (Müller 1780)
- 35(28) Cirrus-pouch extends less than  $\frac{1}{3}$  across breadth of proglottid ..... 36
- 36(39) Testes in 1 layer..... 37
- 37(38) Cirrus-pouch extends  $\frac{1}{3}$ - $\frac{1}{4}$  across the breadth of the proglottid; 10-14 uterine pouches on either side; embryos measure 0.016-0.018 mm. in diameter; cestodes slender.  
*Proteocephalus pinguis* La Rue 1911
- 38(37) Cirrus-pouch extends  $\frac{2}{9}$ - $\frac{1}{7}$  across the breadth of the proglottid; 6-12 uterine pouches on either side; embryos measure 0.0212-0.018 mm. in diameter; cestodes short and robust.....*Proteocephalus cernuae* (Gmelin 1790)
- 39(36) Testes in 2 layers..... 40
- 40(41) Uterine pouches 10 to 16 on either side; cestodes very small and weak.....*Proteocephalus pusillus* Ward 1910

- 41(40) Uterine pouches 3 (or 4) on either side; cestodes large and robust.....*Proteocephalus longicollis* (Zeder 1800)
- 42(27) Testes number more than 70..... 43
- 43(44) Fifth sucker armed with minute hooks or spines.  
*Proteocephalus osculatus* (Goeze 1782)
- 44(43) Fifth sucker unarmed..... 45
- 45(46) Vagina anterior to cirrus-pouch; genital pore posterior to middle of proglottid; suckers 0.25 mm. in diameter.  
*Proteocephalus skorikowi* (von Linstow 1904)
- 46(45) Vagina posterior to cirrus-pouch; genital pore about middle of proglottid; suckers 0.5 mm. in diameter.  
*Proteocephalus pentastoma* (Klaptoez 1906)
- 47( 2) Testes lie in two lateral fields between vitellaria; parasitic in amphibians, aquatic snakes and lizards..... 48
- 48(49) Cuticula of head or of head and parts of strobila covered with minute spines.  
 Genus *Acanthotaenia* von Linstow 1903
- 49(48) Cuticula of neck free from spines or hooks..... 50
- 50(69) Suckers rounded or oval in outline.  
 Genus *Ophiotaenia* La Rue 1911
- 51(52) Vagina always anterior to cirrus-pouch.  
*Ophiotaenia filaroides* La Rue 1909
- 52(51) Vagina either anterior or posterior to the cirrus-pouch..... 53
- 53(62) Genital pore anterior to the middle of margin of proglottid... 54
- 54(57) Uterine pouches 20 or less than 20 on either side..... 55
- 55(56) Head 0.24-0.25 mm. broad; suckers 0.12-0.15 mm. in diameter; testes number 80-100; cirrus-pouch extends about  $\frac{1}{3}$  across the breadth of proglottid.  
*Ophiotaenia nattereri* (Parona 1901)
- 56(55) Head 0.54 mm. broad; suckers 0.27-0.3 mm. in diameter; testes number 100-120; cirrus-pouch extends about  $\frac{1}{2}$  across the breadth of proglottid.  
*Ophiotaenia racemosa* (Rudolphi 1819)
- 57(54) More than 20 uterine pouches on either side..... 58
- 58(61) Testes number about 100-150..... 59
- 59(60) Testes number 100-108, situated in two narrow lateral fields not near vitellaria; several coils of ductus ejaculatorius in base of protruded cirrus.  
*Ophiotaenia trimeresuri* (Parona 1898)
- 60(61) Testes number 90-160, situated in two broad lateral fields extending close to vitellaria, no coils of ductus ejaculatorius in base of protruded cirrus.  
*Ophiotaenia lönnbergii* (Fuhrmann 1895)



- |        |                                                                                                                              |                                               |
|--------|------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------|
| 61(58) | Testes number 150-215.....                                                                                                   | <i>Ophiotaenia perspicua</i> La Rue 1911      |
| 62(53) | Genital pore at or near middle of margin of proglottid.....                                                                  | 63                                            |
| 63(66) | Heads 1.5 mm. or more in breadth.....                                                                                        | 64                                            |
| 64(65) | Muscular wall of suckers of nearly constant thickness about entire circumference; testes number 150-240.                     |                                               |
|        | <i>Ophiotaenia marenzelleri</i> (Barrois 1898)                                                                               |                                               |
| 65(64) | Muscular wall of suckers much thickened on anterior margin; testes number about 200.                                         |                                               |
|        | <i>Ophiotaenia punica</i> (Cholodkovski 1908)                                                                                |                                               |
| 66(63) | Heads less than 1.5 mm. broad.....                                                                                           | 67                                            |
| 67(68) | Testes number 130-160; ductus ejaculatorius forms several coils; 24-35 uterine pouches on either side.                       |                                               |
|        | <i>Ophiotaenia calmettei</i> (Barrois 1898).                                                                                 |                                               |
| 68(67) | Testes number 200-250; ductus ejaculatorius nearly straight; 40-60 uterine pouches on either side.                           |                                               |
|        | <i>Ophiotaenia grandis</i> La Rue 1911                                                                                       |                                               |
| 69(50) | Suckers with point of lower margin re-entrant into cavity of sucker.....                                                     | Genus <i>Crepidobothrium</i> Monticelli 1899. |
|        | The only know species of this genus is                                                                                       |                                               |
|        | <i>Crepidobothrium gerrardii</i> (Baird 1860).                                                                               |                                               |
| 70(1)  | Heads with folds or lappets of tissue about suckers.....                                                                     | 71                                            |
| 71(72) | A single fold of tissue partially covering the base of suckers; head conical.....                                            | Genus <i>Choanoscolex</i> La Rue 1911.        |
|        | The only known species is                                                                                                    |                                               |
|        | <i>Choanoscolex abscisa</i> (Riggenbach 1896).                                                                               |                                               |
| 72(71) | Many folds or lappets of tissue about suckers; anterior surface of head flattened; suckers set in flattened end of head..... | Genus <i>Corallobothrium</i> Fritsch 1886.    |

## DESCRIPTION OF SPECIES

In this section are described the species of the following genera: *Proteocephalus*, sensu strictu, *Choanoscolex* La Rue 1911, and *Ophiotænia* La Rue 1911, of the family Proteocephalidae. The species of *Monticellia* La Rue 1911, belonging in the new family Monticellidae, have also been described. Other species which have been mistakenly placed in the genus *Proteocephalus* have been considered and where possible their rightful position pointed out. The species of *Corallobothrium* and of *Acanthotænia* have not been re-described.

## PROTEOCEPHALUS FILICOLLIS (Rudolphi)

[Figs. 15, 58-60]

1782:	<i>Taenia</i> from <i>Gasterosteus</i>	O. F. Müller	1782:28-29
1786:	<i>Taenia</i> from <i>Gasterosteus</i>	Batsch	1786:241-242
1790:	<i>Taenia gasterostei</i>	Gmelin	1790:3079
1800:	<i>Alyselminthus gasterostei</i>	Zeder	1800:255
1802:	<i>Taenia filicollis</i>	Rudolphi	1802a:114-115
1803:	<i>Halysis gasterostei</i>	Zeder	1803:334
1810:	<i>Taenia filicollis</i>	Rudolphi	1810:106
1819:	<i>Taenia filicollis</i>	Rudolphi	1819:148
1844:	<i>Taenia filicollis</i>	Bellingham	1844:317
1845:	<i>Taenia filicollis</i>	Dujardin	1845:583
1845:	<i>Taenia ambigua</i>	Dujardin	1845:583
1850:	<i>Taenia filicollis</i>	Diesing	1850:512
1850:	<i>Taenia ambigua</i>	Diesing	1850:512
1858:	<i>Proteocephalus ambigua</i>	Weinland	1858:53
1858:	<i>Proteocephalus filicollis</i>	Weinland	1858:53
1872:	<i>Taenia ambigua</i>	Grimm	1872:243-246
1889:	<i>Taenia filicollis</i>	Lönnberg	1889:15
1902:	<i>Taenia filicollis</i>	Schneider	1902:84, 86-87
1905:	<i>Ichthyotaenia filicollis</i>	Schneider	1905:21-24
1909:	<i>Ichthyotaenia ambigua</i>	Lühe	1909:33
1911:	<i>Proteocephalus filicollis</i>	La Rue	1911:473, 474, 475

Specific Diagnosis: Characters of the genus. Very small cestodes. Length as much as 35 mm. or more. Breadth 0.8 mm. Proglottids few, 15-25. Segmentation indistinct. Proglottids attached by their full width. First proglottids broader than long, 0.20 mm. broad by 0.075-0.080 mm. long. Mature proglottids about 0.18 mm. long by 0.370 mm. broad. Ripe proglottids 0.48-0.66 mm. long by 0.425 mm. broad. Head small, 0.090-0.120 mm. broad or perhaps a little more, not always well set off from neck. Suckers 0.042-0.055 mm. in diameter. No fifth sucker present. Neck to first traces of segmentation about 1.0 mm. long.

Genital organs as in genus. Genital sinus marginal, irregularly alternating, situated near middle of segment on a papilla-form prominence. Cirrus-pouch about 0.130 mm. long by 0.032-0.040 mm. broad, reaching about  $\frac{1}{3}$ - $\frac{1}{4}$  across the breadth of the proglottid. Cirrus-canal much coiled in cirrus-pouch. Vas deferens forming mass of eccentric coils. Testes in two layers, about 75-90 in all. Vagina anterior to cirrus-pouch. Sphincter vaginae weakly developed. Receptaculum seminis present. Vitellaria made up of quite compact follicular masses, in lateral fields. Ovary bilobed, connected by an arched mid-piece.

Lobes spheroidal, thick. Uterus when fully developed possessing 5-7-8 lateral pouches on either side. Eggs provided with three membranes. Outermost membrane 0.050-0.075 mm. in diameter, embryonal covering 0.032 mm., embryo 0.027 mm.

Habitat: In intestine of host.

Host	Locality	Collector	Authority
<i>Gasterosteus aculeatus</i> *		Müller	Müller (1782:28-29)
" "	Greifswald	Rudolphi	Rudolphi (1802a:114-115)
" "	Berlin	Olfers	Diesing (1850:512)
" "	Paris	Dujardin	Dujardin (1845:583)
" "	Ireland	Bellingham	Bellingham (1844:317)
" "		Grimm	Grimm (1872:243-246)
<i>Gasterosteus pungitius</i>	Rennes	Dujardin	Dujardin (1845:583)
" "	Halle	Nitsch	Diesing (1850:512)
" "	Greifswald	Creplin	Diesing (1850:512)
" "	Reval, Esthonia		
	(Russian province)	Schneider	Schneider (1905:21-24)
" "	Porkhala, Finland	Levander	Schneider (1902:84, 86, 87)
" "	Upsala	Lönnberg	Lönnberg (1889:15)

O. F. Müller (1782:28-29) stated that he had seen cestodes from the intestine of *Gasterosteus*. He, however, did not describe the species nor did he propose a name for it. One of his drawings of this cestode in its natural size presents so little detail that it is of little value. Müller's *Taenia gasterostei* which he found in the body cavity of *Gasterosteus* is none other than *Schistocephalus solidus*. Batsch (1786:224) and Schrank (1788:49) followed Müller in using this name to designate the cestode found in the body cavity of the stichling. Batsch (1786:241-242) gave but a few notes on Müller's *Taenia* from *Gasterosteus* and he referred to Müller's (1782:28-29) article and figures. Gmelin (1790:3079) used the name *Taenia gasterostei* to designate the cestode found in the intestine of *Gasterosteus aculeatus* by Müller. Gmelin's diagnosis reads: "TAENIA GASTEROSTEI 81.—T. tenuissima, cauda obtusa. Müll. Naturf. 18. p. 28. t. 3. f. 6. 7. Habitat in gasterostei aculeati intestinis, minima, articulis nudo oculo vix discernendis." This name is unavailable because of Müller's prior use of it for the cestode of the body cavity. Zeder (1800:255) in his Nachtrag used the name *Alyselminthus gasterostei* to designate this form. His description is not at hand. Rudolphi (1802a:114-115) gave this species the name *Taenia filicollis*. His specimens came from *Gasterosteus aculeatus* at

\*Type host.



Greifswald. Since this name is here used for the first time Rudolphi's description is quoted in full:

"*Taenia filicollis*: capite globoso distincto; collo longissimo filiformi; articulis ovariisque quadratis.

*Taenia Gasterostei*, Syst. Nat. p. 3079, n. 81.

*Alyselminthus Gasterostei* Zeders Nachtrag, S. 255. Taf. 3. Fig. 1-4.

"Zu dem, was aus Goezes nachgelassenem Manuscript bey Zedern gesagt ist, habe ich wenig hinzuzusetzen. Ich habe diesen Wurm nur sehr selten in Darmkanal des Sticlilings gefunden, und noch immer durch einen unglücklichen Zufall ohne den Kopf. Der Hals ist lang, dünn und ungegliedert; die Glieder des Körpers bis auf das letzte, welches stumpf abgerundet ist, viereckig. Da die Eyerstöcke so sehr ausgezeichnet sind, wundert es mich, dass er ihrer gar nicht erwähnt, so wie auch die Worte, *Glieder hat der Wurm eigentlich nicht*, mir unverständlich sind, da die Glieder sehr deutlich sind. Die Eyerstöcke sind viereckig, und zwar mit hervorstehenden Ecken, so dass sie auf den vier Seiten einen hellen Fleck übrig lassen, da sie selbst weiss und undurchsichtig sind. Jedes Glied ist also von dem andern durch einen hellen Fleck abgesondert, und an den Seiten des Wurms läuft eine unterbrochene helle Linie, wodurch diess Thierchen ein sehr schönes Ansehen bekommt."

Zeder (1803:334) gave a brief diagnosis of this species which he called *Halysis gasterostei*. He referred to the writings of Müller (1782), Batsch (1786), Zeder (1800), Gmelin (1790). He stated that its habitat was the intestine of *Gasterosteus aculeatus*. Rudolphi (1810:106) gave a diagnosis, description, and synonymy of this species. His synonymy shows very clearly that he himself considered his species to be identical with the forms which earlier workers had described as *Taenia gasterostei* (the intestinal parasite) and *Alyselminthus gasterostei*. Rudolphi's diagnosis and description are here quoted:

"*Taenia filicollis* R. *Taenia*: capite subgloboso discreto, collo longissimo, filiformi, articulis, ovariisque quadratis. Müller im Naturforscher St. 18. p. 28. Tab. 3, fig. 6. 7. *Taenia ex intest. Gasterostei*. Batsch Bandw. p. 241, n. 14. Gmel. Syst. Nat. p. 3079, n. 81. *Taenia gasterostei*. Goeze apud Zederum in huj. Nachtrag, p. 255. Tab. 3. fig. 1-4. *Alyselminthus Gasterostei*. Rudolphi in Wied. Arch. III. 1, p. 114. *Taenia filicollis*. Zeder Naturg. p. 334, n. 10. *Halysis Gasterostei*.

"Hab. In *Gasterostei aculeati* intestinis Goezius Augusto, ipse aliquoties sed capite orbam, Iunio, reperimus.

"Descr. Vermes duos tresve pollices longi, fere lineam lati, candidissimi.

"*Caput* subglobosum, discretum, *osculis* orbicularibus, majusculis, binis tam superioribus, quam inferioribus. *Collum* filiforme, longissimum. *Corpus* planum articulis anticis minoribus, reliquis subaequalibus, quadratis, ultimo rotundato. *Ovaria* quadrangularia, angulis acutis productis, opaca, ut articulorum tantum partes inter angulos sitae pellucidae sint. Vermis inde aspectus lepidus, inter

quoslibet enim articulos maculae pellucidae, et simul canalis lateralis pellucidi species oboritur. Foramina non visa.

"Obs. 1. Goezius, qui ovária non vidit, vermem proprie non articulatam esse in posthumis reliquit, ipse vero hanc speciem aequae ac ullam aliam articulatam observavi. A Bothriocephalo solido, in Gasterostei abdomine hospitante, omnibus prorsus notis diversissima.

"Obs. 2. Vermem in aqua fluviali biduum vixisse, in puteali enecari. Goezius observavit."

Rudolphi (1819:148) adds nothing to his former data. Bellingham (1844:317) in his catalogue of Irish Entozoa reported the finding of *Taenia filicollis* in the intestine of *Gasterosteus aculeatus*. His observations added nothing to our knowledge of the structure of the worm. Dujardin (1845:583) reported that he had found *Taenia filicollis* in *Gasterosteus aculeatus* at Paris in 1838. His description, a part of which seems to have been derived from Rudolphi (1810) reads:

"Long de 50 à 80 mm., large de 2 mm. environ; tête presque globuleuse, distincte et portée par un cou très-long, filiforme;—sans trompe;—articles presque carrés, contenant des ovaires (?) opaques également carrés, qui laissent entre eux, et sur les bords, des intervalles demi-transparents."

"Rudolphi et Goeze l'ont trouvé en Allemagne, dans le *Gasterosteus aculeatus*. Je l'ai trouvé aussi dans ce poisson, à Paris, en 1838; j'y ai vu des oeufs à double enveloppe, dont l'externe, mucilagineuse, est longue de 0 mm, 06 à 0 mm, 10; l'enveloppe interne, globuleuse, est large de 0 mm, 036, et les crochets de l'embryon sont longs de 0 mm, 012."

Dujardin (1845:583) also described a form from *Gasterosteus pungitius* (*laevis*) which he named *Taenia ambigua*. His specimens were collected at Rennes, France. His description reads:

"Long de 6 mm, large de 0 mm, 5 à 0 mm, 8, formé de quinze à dix-sept articles peu distincts et de forme très-variable;—tête petite, large de 0 mm, 17, sans trompe et sans crochets tantôt rétractée tantôt saillante, quelquefois globuleuse et séparée, par un cou très-étroit, quelquefois à quatre lobes distincts, correspondant aux ventouses larges de 0 mm, 068 à 0 mm, 07;—cou très-contractile et dilatable, traversé par quatre canaux larges de 0 mm, 009;—premiers articles mâles avec les orifices génitaux irrégulièrement alternes, et les pénis longs de 0 mm, 16, larges de 0 mm, 032, ridés transversalement;—derniers articles informes, remplis d'oeufs globuleux à double enveloppe;—enveloppe externe mucilagineuse, longue de 0 mm, 053 à 0 mm, 058;—enveloppe interne longue de 0 mm, 034; embryon de 0 mm, 026, avec des crochets de 0 mm, 0095."

"Je l'ai trouvé plusieurs fois à Rennes dans l'intestin du *Gasterosteus laevis*. Son nom spécifique exprime sa ressemblance avec les scolex et les caryophyllés."

If Dujardin's description of his *T. filicollis* and his *T. ambigua* be compared, it will be noted that in the measurements of the second egg membrane there is very good agreement. The variation in the size of

the outer egg membranes in *Proteocephalus* is large, hence but little value can be given to that measurement. Unfortunately Dujardin failed to give the measurements of the embryo in either case, so no comparison in that respect is possible. Dujardin records a difference of 0.0025 mm. in the length of the hooks of the embryos of the two species. That measurement, however, is difficult to make with accuracy and little weight should be given it as a means of differentiating the species. It is probable that Dujardin's specimens from *Gasterosteus aculeatus* and from *G. pungitius* belonged to the same species. Weinland (1858:53) made *Taenia ambigua* Dujardin the type of his genus *Proteocephalus* and with that species he included *Taenia filicollis* and *Taenia dispar*.

Diesing (1850:512) recording *Taenia filicollis* Rud. added nothing to Rudolphi's diagnosis and description of that species. He gave a complete synonymy up to his time, and stated that this species had been found in the intestine of *Gasterosteus aculeatus* in August by Goeze and in June at Greifswald by Rudolphi; in September at Berlin by de Olfers; at Paris by Dujardin; in *Gasterosteus pungitius* at Halle by Nitsch; at Greifswald by Creplin. Concerning *Taenia ambigua* Diesing (1850:512) gave nothing new.

Grimm (1872:243-246) found a form in *Gasterosteus aculeatus* which he identified as *Taenia ambigua* Dujardin. Grimm published no drawings of his specimens. The important parts of his description are here quoted:

"TAENIA AMBIGUA Duj.:—Im Darne des bei uns so häufig vorkommenden Stichlings (*Gasterosteus aculeatus*), von denen ich in vergangenen Sommer mehr als 100 aufgeschnitten habe, fand ich unter andern 6 Exemplare einer Bandwurmgattung. Sie unterscheiden sich sehr leicht von allen ihren Verwandten und sind augenscheinlich zu der von Dujardin aufgestellten Species *Taenia ambigua* zu rechnen, obgleich die Bestimmung, einer kurzen Beschreibung des äusseren Habitus nach, höchst schwierig ist und sehr leicht zu einen Irrthum führen kann.

"Das grösste von mir aufgefundene Exemplar hatte 30 Mm Länge und 1 Mm Breite. Die Grossenverhältnisse der einzelnen Körpertheile eines 11,5 Mm langen Exemplars sind folgende; die Länge des Köpfchens—0.13 Mm, dessen Breite—0.25 Mm, dessen Dicke—0.15 Mm, der Durchmesser der Saugnäpfe—0.25 Mm, die Länge des Halses—1.1 Mm, die Länge der ersten unreifen Glieder 0.014 Mm; dieselben verlängern sich allmähig, indem sie 0.02 Mm., 0.03 Mm u. s. w. lang werden; reifere Glieder, ungefähr aus der Mitte des Wurms, haben eine Länge von 0.20 M., und das vollkommen reife vorletzte Glied ist 0.43 Mm. lang. Die Dicke des Wurmkörpers steigt bis zu 0.5 Mm.

"Das Köpfchen des Wurms von der Seite betrachtet, erscheint etwas angeschwollen; wenn man es von der Fläche betrachtet, so sieht man an den in Weingeist conservirten Exemplaren eine Furche, die über den Kopf, an dessen freiem Ende, von der einen flachen Seite des Wurms zur andern verläuft. Diese Furche ist aber gewiss keine constante Bildung, wird aber dadurch hervorgerufen, dass



der Wurm, überhaupt sehr contractil, sein Köpfchen ofters einzieht, namentlich wenn er in Weingeist gelegt wird. Einen Rüssel besitzt er nicht. Die Saugnäpfe, die eine runde Form haben, sind paarweise auf den den flachen Seiten des Körpers entsprechenden Kopftheilen angeordnet. Die Geschlechtsöffnungen liegen am Rande der Glieder, eine über der andern. Alle Glieder, die mit dem Alter allmählig breiter werden, haben eine ziemlich unregelmässige Form, besonders aber ihre Ränder. Die Farbe des Wurms ist rein weiss. Indem wir noch hinzusetzen, dass das letzte Glied an seinem hintern Rande beständig etwas aufgeschlitzt ist, haben wir eine möglichst vollständige Darstellung des Aeussern des Bandwurms geliefert.

“Dieser Bandwurm ist höchst zart . . . .—

“Von dem weiblichen Geschlechtsorgan habe ich nur die Keimdrüse und den Uterus aufgefunden; die Keimdrüse liegt in der Mitte des Gliedes und hatte in dem untersuchten Stadium ein spindelförmiges Aussehen; von ihr geht der Uterus aus, der aus einem Röhre mit feinen faserigen Wandungen besteht, das mehrere Schlingen bildet. Der Uterus verläuft in die Scheide, die sich zum Seitenrande des Gliedes biegt, wo sie nach aussen mit einer ziemlich grossen Oeffnung mündet.

“Neben dem weiblichen Geschlechtsporus liegt eine andere Oeffnung, die in das männliche Geschlechtsorgan führt. Das letzte besteht aus dem kolbenförmigen Cirrusbeutel mit dem nach innen gewendeten Cirrus, der an seinem Ende etwas anschwillt. Hinter dem Cirrusbeutel liegt die doppelte Samendrüse.

“In dem letzten, also am meisten entwickelten Gliede waren nur Keime, nicht aber entwickelte Eier zu sehen.”

Von Linstow (1878:231) reported as hosts for *Taenia filicollis* and *Taenia ambigua* only those which had been reported by Diesing (1850). Zschokke (1884:16-17) reported and briefly described a cestode from *Perca fluviatilis*, Lake Lucerne, which he considered to be *Taenia filicollis* Rud. His specimens probably belonged to *Proteocephalus dubius* La Rue. Leidy (1886:62-63) thought that he had found *Taenia filicollis* in the intestine of *Amia calva* from North Carolina. His specimens probably belonged to the species for which La Rue (1911) proposed the name *Proteocephalus perplexus* La Rue. Lönnberg (1889:15) reported the finding of *Taenia filicollis* in *Gasterosteus pungitius* at Upsala. He added a very little to Rudolphi's diagnosis.

Kraemer (1892) reported and described a form from the intestine of *Coregonus fera*, Lake Lucerne, which he first identified as *Taenia filicollis* Rud. In the same paper Kraemer showed that his *Taenia filicollis* and his *Taenia ocellata* were identical. Riggenbach (1896) and Benedict (1900) accepted Kraemer's determination. This species has been shown to differ from the *Taenia filicollis* of Rudolphi and is described under the name *Proteocephalus fallax* La Rue 1911, where a full discussion of the position of Kraemer's species may be found. Benedict

(1900) described an American species of cestode under the name *Proteocephalus filicollis* (Rud.). In a note he changed the name to *Proteocephalus ocellata* (Rud.). He accepted Kraemer's statement that Rudolphi's *Taenia ocellata* and *T. filicollis* were identical. For this form which proves to be a new species La Rue (1911) proposed the name, *Proteocephalus exiguus* La Rue. Schneider (1902:21-23) reported a parasite from *Perca fluviatilis*, in Finland, as *Ichthyotaenia filicollis* (Rud.). This form he later (1903:13 and 1905:15-17) considered to be identical with O. F. Müller's *Taenia percae*. Schneider (1902:84, 86-87) reported a specimen from *Gasterosteus pungitius* as *Ichthyotaenia filicollis* (Rud.). In a later paper (1905:21-24) he considered this form to be *Ichthyotaenia ambigua* Dujardin and here he gave the first good description of this species. Lühe (1909) gave a diagnosis of this species under the name *Ichthyotaenia ambigua* Dujardin. His diagnosis added nothing to the data given by Dujardin (1845) and Schneider (1905). La Rue (1911:473, 474, 475) presented some of the conclusions that are given in the present paper at greater length.

The name *Taenia gasterostei* as proposed by Gmelin (1790) for this species is not available because it was first used by Müller (1782) to designate the species now known as *Schistocephalus solidus*. For the same reason the name *Alyselminthus gasterostei* Zeder (1800) is rendered invalid. The name *Taenia filicollis* Rudolphi (1802) being first used to indicate this species remains available. The generic name is *Proteocephalus* as indicated by Weinland (1858). It is of importance here to determine the systematic position of the specimens reported by Grimm (1872) and by Schneider (1902 and 1905). A careful comparison of their descriptions with Dujardin's (1845) description of *Taenia ambigua* shows that they evidently belong to the latter species. One notes that Grimm's material was found in *Gasterosteus aculeatus* while Schneider's specimen came from *G. pungitius*, and a consideration of these data at once precipitates the question as to the possibility that *T. ambigua* Dujardin and *T. filicollis* Rudolphi might not prove to be identical and hence synonymous. The answer to this question must be sought in the study of the collection records and in a comparison of the structures of the forms involved.

In regard to habitat one may present certain general considerations that should have weight. The identity of the two forms can not be considered proven because they have been found together in a single host or separately in different members of a host species, for numerous instances could be cited in which a species or an individual of that species served as host for two or more closely related species of cestode. Nevertheless, it is true that a knowledge of the host is considered to

have an important bearing on the proof of an identity. Frequently the knowledge that two forms have the same species for a host furnishes the first intimation that they may prove to be identical.

One may also make the statement that the finding of specimens apparently belonging to the same species in two or more unrelated host species may give an early intimation that these specimens belong to different species. While it is true that certain cestodes seem to be limited in their habitat to a single host species there is a sufficiently large body of facts to warrant the belief that in general cestode species are not so limited. It is of common acceptance that closely allied hosts having a wide distribution and inhabiting the same regions and especially when they have similar feeding habits very frequently harbor the same species of parasites.

*Gasterosteus aculeatus* and *G. pungitius* are closely allied, have wide distribution, inhabit the same region, and have similar feeding habits. *Taenia ambigua* has been reported from *G. aculeatus* by Grimm and from *G. pungitius* by Dujardin and Schneider. *Taenia filicollis* has been reported from *G. aculeatus* by Rudolphi, Goeze, Diesing, Dujardin, and Bellingham, and from *G. pungitius* by Diesing (from specimens collected by Nitsch and Creplin) and Lönnberg. So far as hosts are concerned there is evidence to believe that *Taenia filicollis* and *Taenia ambigua* are identical species. Against this identity is the fact that Dujardin's description of *T. filicollis* indicates a larger form than does his description of *T. ambigua*. It is a well-known fact, however, that a considerable variation in length and breadth may exist in the same species of cestode. These discrepancies in size may be due to the degree of maturity and to the contraction states of the individual worms. It is not known whether Dujardin's specimens of *T. ambigua* had attained their full development nor is this known concerning the specimens described by Grimm or Schneider. There are no statements to show whether Dujardin measured his specimens while alive or after preservation. This would make a real difference.

Attention has already been called to the fact that in regard to the egg measurements made by Dujardin for the two forms in question there is pretty good agreement. There is not sufficient evidence at hand to prove positively that *Taenia ambigua* is identical with *Taenia filicollis*, yet it seems that the evidence for the identity is stronger than the evidence against it. Therefore in this work the writer will consider that these species are identical and since *Taenia filicollis* has the right of priority that name should be retained. It is to be hoped that this discussion, which in no way can be considered to settle the problem of the identity of these species, will be the incitement to a genuine compara-



tive study of the cestodes of *Gasterosteus aculeatus* and *G. pungitius*. There is doubtless a large amount of such material already brought together in the museums and private collections of Europe upon which an investigator could work.

Schneider's material was found for the most part in *Gasterosteus pungitius* from Obersee near Reval, Esthonia (a province in Russia) in the months of May and June. Never more than four cestodes of this species were found in a single host. He also studied a single specimen found by Dr. K. M. Levander in *Gasterosteus pungitius*. This specimen was reported by Schneider (1902:84, 86-87) as *Ichthyotaenia filicollis* (Rud.). For my study Dr. H. B. Ward very kindly secured one of Schneider's specimens of this species, stained in carmine and mounted in toto, from Dr. K. M. Levander in Helsingfors. It bears the label, "Ichthyotaenia ambigua, int. Gast. pungitius 23/10 VI, 04." The description which follows is based on Schneider's (1905:21-24) description and on the writer's observations on this one mounted specimen.

Schneider's longest specimen measured as much as 35 mm. long by a maximum breadth of 0.8 mm. and it possessed 17 proglottids. Of these the anterior were broader than long and they were united by their whole width. Proglottids well filled with eggs are longer than broad and have a well rounded outline. The specimen studied by the writer has about 25 proglottids. Of this number but a few at the anterior end are young. These are followed by a large number of nearly mature and mature proglottids and these in turn by a small number of ripe proglottids. The strobilation is indistinct. The first proglottids measure about 0.075-0.080 mm. long by 0.200 mm. broad while the mature proglottids measure about 0.180 mm. long by 0.370 mm. broad and the ripe ones about 0.48-0.660 mm. long by 0.45 mm. broad. An end proglottid tapers posteriorly and is 0.975 mm. long by 0.425 mm. broad. Schneider states that the scolex is small, 0.100-0.120 mm. broad, and not well set off from the neck. The suckers measure 0.055 mm. in diameter. No fifth sucker is present. The neck is relatively broad and its length is about one-fourth that of the body. In the specimen examined by me the breadth of the head at the base of the suckers is 0.090 mm. It is very short and not well set off from the rather broad neck. Suckers are about 0.042 mm. in diameter over all. The first traces of segmentation occur at a point about 1.0 mm. behind the head. This makes the neck equal to about  $\frac{1}{8}$  the length of the entire body.

It is stated by Schneider that the excretory vessels are quite wide; that the two ventral vessels which communicate in each segment with the exterior through a submarginal pore measure 0.03 mm. in diameter; and that the dorsal vessels are smaller, their diameter being 0.0075 mm.

The genital pore is marginal, irregularly alternating, and situated about the middle of the proglottid length. It is rather prominently situated on a little eminence which is most evident in ripe proglottids. This eminence may be caused by a pushing out of that region by nearby organs.

The cirrus-pouch measures about 0.130 mm. long by 0.032-0.040 mm. broad. Its length goes into the proglottid breadth from three to four times. The cirrus-canal, as Schneider states, is greatly coiled within the cirrus-pouch and it broadens out at its proximal end to form a vesicula 0.030 mm. broad. Coils of the vas deferens form a mass which lies toward the porose side of the proglottid. The testes in the preparation examined by the writer lie in two layers of about 35-50 testes each. Thus the total number of testes is about 75-90 or more. Schneider found that the testes measure 0.055-0.062 mm. in sagittal and 0.035-0.045 mm. in frontal diameter.

The vagina lies anterior to the cirrus-pouch. Schneider found a weak sphincter vaginae near the vaginal opening. It was not visible in the specimen which the writer studied. The vagina passes in a curve to the middle of the segment and thence posteriad to the interovarial space. Schneider found a small receptaculum seminis just anterior to the ovary. The vitellaria are quite compact follicular masses in the lateral fields of the segments. Of the ovaries Schneider writes, "The ovaries appear as spherical bodies when seen from the surface. In the posterior segments, after they have filled the uterus with eggs, they wither completely or the remains of the genital organs, pressed together into a triangular area, are recognizable as two small round bodies in the posterior region of the segment. I hold that Grimm (1872, p. 246) erroneously considered this triangular area to be the ovary when he says: 'the ovary lies in the middle of the segment and has in its observed condition a spindle-like appearance' ". The ovary is bilobed, the somewhat spheroidal lobes being connected by a short arched mid-piece. In the ripe proglottids observed by me the ovary could still be distinguished. The uterine passage was found by Schneider opening into the uterus posterior to the middle of the proglottid and opposite to the pre-formed opening of the uterus to the exterior. When immature the uterus is a median tube but when fully developed it has 5-7-8 lateral pouches on either side.

As observed by Schneider the outer membrane of the egg has a diameter of 0.050-0.075 mm. The embryonal covering measures 0.032 mm. and the embryo itself 0.027 mm. These measurements of the egg agree pretty well with the measurements as given by Dujardin (1845). The embryos especially agree well in size, and it may be pointed out that this is of importance in seeking to prove an identity.

*P. filicollis* somewhat resembles *P. agonis* Barbieri but it may be differentiated from that species by its relatively shorter cirrus-pouch, by a different position of the mass of coils of vas deferens, by its larger testes which are arranged in two layers while the testes of *P. agonis* are in one layer. *P. agonis* has no genital papilla while in *P. filicollis* there is a simulation of one. *P. filicollis* is readily distinguished from *P. dubius* La Rue and *P. fallax* La Rue by its smaller size, by its lack of a fifth sucker, by its more numerous testes, shorter cirrus-pouch and smaller proglottids. The embryos of *P. filicollis* are smaller than those of *P. fallax*. *P. filicollis* differs from *P. pusillus* Ward and *P. exiguus* La Rue in not having a fifth sucker, in having smaller suckers, a smaller head, more testes, and fewer uterine pouches. *P. filicollis* differs greatly from *P. percae* in the lack of a fifth sucker, in the size of body, head and suckers, in the proportions of the proglottids, in the size of the cirrus-pouch, ovaries, etc. It likewise differs from *P. cernuae* in practically the same points as stated for *P. percae*. *P. filicollis* is smaller than *P. esocis*. It has a shorter cirrus-pouch and a larger number of testes. The proportions of the proglottids are different. The two species are alike in not possessing a fifth sucker.

#### PROTEOCEPHALUS ESOCIS (Gui. Schneider)

[Figs. 16, 61-63]

1905: *Ichthyotaenia esocis* Gui. Schneider, 1905:19-20

1911: *Proteocephalus esocis* La Rue, 1911:475

Specific Diagnosis: The characters of the genus. Cestodes small and slender, 1-4.7 cm. long, maximum breadth 0.7 mm. Scolex 0.140 mm. broad, 0.105 mm. thick. No fifth sucker, nor vestige of it. Suckers shallow, weak, small, about 0.050 mm. in diameter, directed anteriad. Diameter of sucker opening 0.026-0.032 mm. Neck 2-5 mm. long. Sixty-six proglottids in specimen 4.7 cm. long, youngest proglottids twice as broad as long, 0.370 mm. broad by 0.170 mm. long. Middle proglottids broader than long, 0.680 mm. broad by 0.390 mm. long. Last proglottid longest, 0.650 mm. long by 0.460 mm. broad at anterior end. Segmentation not evident. Transverse intersegmental furrows shallow. Surface smooth.

Genital organs as in genus. Genital pore not on genital papilla. Pore marginal, irregularly alternating, about middle of proglottid. Cirrus sheath relatively long, extending nearly to middle of proglottid. Length of cirrus-pouch 0.230-0.250 mm. Cirrus sinuous. Vas deferens, a mass of coils in middle of proglottid. Testes, 30-38 visible in mature



proglottids, 44-52 in young proglottids. Testes arranged in two partial layers between vitellaria. Diameter of testes, 0.050-0.090 mm. Vagina anterior to cirrus-pouch. Near vaginal opening a small sphincter vaginae. Receptaculum seminis anterior to ovary. Passages in inter-ovarial space as in genus. Ovary bilobed, lobes ovoidal, vitellaria sparse, follicles small. Uterus not observed. Two pairs of excretory vessels, ventral and dorsal. Dorsal vessels small, ventral vessels much larger.

Habitat: In intestine of *Esox lucius* L. (type host); Reval, Esthonia (type locality).

This species was described and delineated by Gui. Schneider (1905: 19-20). La Rue (1911:475) included it in a list of species belonging to the genus *Proteocephalus*.

This species from *Esox lucius* taken at Reval in Esthonia, a province of Russia, Apr. 30, 1904, is briefly described by Gui. Schneider (1905). Thanks to Dr. H. B. Ward the writer has had some of Schneider's preparations and alcoholics for examination. The paucity of alcoholic specimens prevented the use of the section method. The writer has therefore been compelled to be content with a study of toto preparations and specimens cleared in glycerine. The description following is based largely on Schneider's data tho wherever possible the writer has introduced his own findings.

The worms are small and slender 1-4.7 cm. long. A maximum breadth of about 0.7 mm. was observed. No worms had ripe proglottids. The diameter of the scolex is about 0.140 mm. The four shallow suckers directed partly forward are weak, small, and about 0.05 mm. in diameter. A vestigial fifth sucker is lacking, tho perhaps a slight thickening of cells in the anterior part of the head is to be considered as the vestige of the shrunken sucker (Schneider). My measurements of a head and its suckers are: breadth 0.140 mm., thickness 0.105 mm., diameter of suckers 0.053 mm., diameter of sucker openings 0.026-0.032 mm. A most careful search of Schneider's toto preparation and of the specimen cleared in glycerine failed to reveal a trace of a fifth sucker or vestige of it. The last might not have been visible under these conditions. A functional fifth sucker certainly is not present. The suckers are quite prominent, the sucker cavities shallow. The slightly depressed head possesses a short flattened tip. The head is not well set off from the neck. Schneider says that the length of the neck is about  $\frac{1}{3}$  the length of the body. The writer finds it to be from 2.5-3-4.5 mm.

Schneider's largest specimen, 4.7 cm. long, was made up of 66 proglottids. The youngest proglottids were about twice as broad as long, the middle ones somewhat broader than long, and the posterior

ones quadrate or a little longer than broad. The intersegmental furrows were not plain. The measurements of the proglottids in a glycerine specimen examined by the writer were as follows: First proglottids 0.370 mm. broad by 0.170 mm. long, middle and mature proglottids 0.680 mm. broad by 0.390 mm. long. The last proglottid in the strobila was the longest, measuring 0.650 mm. long by 0.460 mm. broad at anterior end. The segmentation is not evident. The proglottids are joined by their full breadth and the transverse furrows between the segments are very shallow. No longitudinal furrows are present. Drawings of three regions (Figs. 61, 62, 63) show the proportions of the segments at anterior, post-middle, and posterior region.

The genital pore, not marked by a papilla, is marginal, irregularly alternating in the strobila, and is situated about the middle of the proglottid. The cirrus-sheath is relatively very long and slender, for it extends about to the middle of the proglottid. Its length in the broadest proglottids is about 0.230-0.250 mm. Schneider reports that its inner end lies very near the dorsal muscle layers. This is also the case in *P. percae*, *P. pinguis* La Rue, *P. exiguus* La Rue and a number of other *Proteocephalus* species. The cirrus runs through the cirrus-pouch in a sinuous course without the formation of a vesicula seminalis. The vas deferens forms a fairly large mass of coils in the middle of the segment. This mass however is much smaller than in *P. fallax* La Rue or in *P. exiguus* La Rue. Schneider found about 30 testes in each segment, lying in a single layer, about 8 in a transverse row, and they measured 0.080-0.090 mm. in sagittal by 0.040-0.050 mm. in frontal diameter. It has been found difficult to count the testes in the more mature proglottids. Thirty-eight testes are shown in nearly mature proglottids (Fig. 62) while in the younger proglottids where they are smaller and more easily distinguished the writer counted 44-48-52. The testes seemed to be in two partial layers filling the area between the vitellaria. The larger testes measure as much as 0.070-0.080 mm. tho the larger number measure about 0.050 mm. Schneider found the diameter of the two ventral excretory vessels to be about 0.015 mm. and that of the two dorsal about 0.0025 mm.

The vagina (Fig. 62) opens anterior to the cirrus-pouch. Very near the opening, 0.030 mm. from it, is a sphincter muscle 0.015 mm. thick, according to Schneider. The writer was unable to observe this. From its opening the vagina as a broad tube describes a long smooth curve to the middle of the proglottid, then it bends posteriad and passes back to the interovarial space. As the vagina nears the middle of the segment the lumen becomes constricted. Early in its course it crosses the cirrus-pouch diagonally. The vagina is dorsal to the uterus.

Schneider found a small receptaculum seminis just anterior to the ovary. According to Schneider the passages in the interovarial space bear the relations customary to Proteocephalids. The ovary is bilobed, the lobes being like two elongated balls connected by a slender arched mid-piece. The vitellaria are lateral, follicular, sparse, and the individual follicles are small. The uterus was not observed by Schneider. It is not well developed in any of the specimens examined by the writer. Schneider saw the opening of the uterine passage and the pre-formed uterus opening just a little posterior to the middle of the proglottid. No eggs were seen. No proglottids were ripe.

This species is quite closely allied to the *P. filicollis* (Rud.) = (*ambiguus*) described by Gui. Schneider (1905). However it is differentiated from *P. filicollis* by its much longer cirrus-pouch and by its larger testes. *P. filicollis* (Schneider's specimen) shows a slight genital prominence upon which the genital pore is situated. It differs very markedly from the *P. pinguis* La Rue found in our North American *Esox lucius*. The *P. pinguis* is a larger worm with a larger head, larger suckers, a functional fifth sucker, a relatively shorter cirrus-pouch, and a larger number of testes. *P. fallax* La Rue, *P. exiguus* La Rue, *P. pusillus* Ward, and *P. percae* (O. F. Müller) are readily distinguished from *P. esocis* by means of the fifth sucker and many other characteristics which are best shown in the comparative tables. *P. macrocephalus* (Creplin), a form without a fifth sucker, is much larger, has more numerous testes, a relatively shorter cirrus-pouch and in other ways also it differs widely from *P. esocis* (Schneider).

#### PROTEOCEPHALUS AGONIS (Barbieri)

[Figs. 158, 174, 185]

1909: *Ichthyotaenia agonis* Barbieri, 1909:334-341

1911: *Proteocephalus agonis* La Rue, 1911:475

Specific Diagnosis: Characters of the genus. Cestodes of small size. Strobila 3-4 cm. long, maximum breadth of same about 0.5 mm. Scolex small, 0.168 mm. in diameter, unarmed. No fifth sucker. Suckers circular, symmetrically arranged on head, size? Neck quite long, as much as 3 mm., breadth 0.140 mm. Neck not well differentiated from strobila. Proglottids very variable in form and number. At times as many as 50-70. First proglottids broader than long. Mature proglottids longer than broad, 0.580-0.620 mm. long by 0.330-0.370 mm. broad. Ripe proglottids filled with eggs, nearly quadrate, length and breadth about 0.5 mm.



Genital aperture marginal, irregularly alternating, situated near middle of proglottid length. Male organs as in genus. Testes spherical, 0.031-0.038 mm. in diameter, about 100 in number. Testes packed in area between vitellaria. Coils of vas deferens in middle of proglottid. Ductus ejaculatorius nearly straight. Cirrus straight, with a thick wall. Cirrus-pouch ovoidal, broad at inner end, extending to middle of proglottid. Female organs as in genus. Vagina always anterior to cirrus-pouch. Uterus in ripe proglottids made up of 4-6-8 lateral pouches on either side. Diameter of eggs 0.037-0.038 mm.

Habitat: In intestine and pyloric coeca of *Alosa finta* var. *lacustris* Fa. (type host); Lake Como, Italy (type locality).

The material was collected by Prof. Ciro Barbieri at Bellagio on Lake Como in Italy from the intestines and pyloric coeca of *Alosa finta* var. *lacustris* Fa. He found them here in great numbers, up to 1200-1400 in a single host.

Barbieri (1909) described this species. La Rue (1909:475) included it in a list of species of *Proteocephalus*. Since it was impossible to secure specimens for study the present description is based upon Barbieri's description.

The scolex (Fig. 158) is very small, with a diameter of about 0.168 mm. It is unarmed and has no fifth sucker. The four suckers are circular in outline and they are symmetrically arranged on the head. The neck, which is about 3 mm. long and 0.140 mm. broad, is not well differentiated from the strobila. The proglottids are very variable in number and form. One well developed individual with ripe eggs in the last proglottid had 50-70 proglottids. The first proglottids are broader than long. Mature proglottids are longer than broad, 0.580-0.620 mm. long by 0.330-0.370 mm. broad. Ripe proglottids filled with eggs are nearly quadrate, length and breadth being about 0.5 mm. The length of the worm is variable. Well developed individuals measure 30 mm. long while a single individual measured 40 mm.

The genital aperture is marginal, irregularly alternating, situated about the middle of the length of the proglottid, and marked by a shallow depression. The testes (Fig. 185) fill the whole area between the vitellaria anterior to the ovary. They are nearly spherical, 0.031-0.038 mm. in diameter. Barbieri figures about 100 testes. The coils of the vas deferens form a thick mass which occupies the middle region of the proglottid. Its walls are thin and its lumen large. The ductus ejaculatorius has a sinuous course in the inner two-thirds of the cirrus-pouch but apparently it forms no closely twisted coils before it passes over into the straight heavy-walled cirrus. The cirrus-pouch extends

to the middle of the proglottid. It is ovoidal with its broadest part at the inner end. Its wall is thick, thickest at the outer end.

The ovary is bilobed, the lobes being oval in shape with smooth outlines. The vitellaria are lateral, longitudinal, follicular glands which lie just inside of the lateral ducts. Oviduct, oötype, and other organs of the interovarial space are as in other species of the genus. The vagina (Fig. 185) always lies anterior to the cirrus-pouch. It widens slightly and again narrows in its course to the middle of the proglottid. Near the inner end of the cirrus-pouch it bends posteriorly and thence takes a direct course to the interovarial space where it forms several coils. The uterus (Fig. 174) containing eggs is made up of 4-6-8 lateral pouches which in fully ripened segments fill up the space between the vitellaria.

The excretory system is of the usual type. Two pairs of lateral excretory ducts take their origin in the head region. They empty into a small bladder situated at the base of the last proglottid. No secondary openings were observed in the head but they were found in the posterior region of each proglottid.

The eggs have a diameter of 0.037-0.038 mm. Barbieri failed to state whether this measurement included only the embryo or embryo with its membranes. Larval stages were found in *Bythotrephes* and *Leptodora*.

This species, as will be seen from its position in the tables at the end of this section, is most closely related to *P. esocis* (Schneider). It is differentiated from that species by its different proportions, by its much smaller and more numerous testes, by the position of the coils of the vas deferens and by the relation of the vagina to the cirrus-pouch. *P. agonis* while resembling *P. filicollis* in size differs from that species in having a longer cirrus-pouch, in the excentric position of the coils of vas deferens, and in having smaller and more numerous testes which lie in one layer. *P. agonis* is readily distinguished from *P. fallax*, *P. dubius*, *P. pusillus*, and *P. exiguus* by its lack of a fifth sucker, by its more numerous and smaller testes, and by its less numerous uterine pouches.

## PROTEOCEPHALUS EXIGUUS La Rue

[Figs. 14, 50-52, 118, 135-138]

1900: *Proteocephalus flicollis* Benedict, 1900:355-3651911: *Proteocephalus exiguus* La Rue, 1911:477-478

Specific Diagnosis: Characters of genus. Strobila short and slender. Length 9-15-25-38 mm. Maximum breadth 0.425-0.646-0.8 mm. Segmentation not evident. Intersegmental furrows shallow. Neck 2-4-7-10(?) mm. long by 0.10-0.20 mm. broad. First proglottids longer than broad or nearly quadrate. Mature and ripe proglottids longer than broad. Ripe proglottids considerably larger than mature ones, 0.680-1.190 mm. long by 0.460-0.595 mm. broad. End-proglottid elongated, pointed posteriorly, 0.714-1.50 mm. long by 0.40-0.646 mm. broad. Head somewhat globular, flattened dorsoventrally, bearing four suckers on its broadest part. Breadth of head 0.120-0.160-0.170 mm. Suckers 0.058 mm. broad by 0.069-0.085 mm. long. Opening of suckers about 0.040 mm. in diameter. Fifth sucker muscular, functional, 0.037-0.048 mm. in diameter. Common genital sinus alternating irregularly, situated near middle of lateral margin of proglottid. Testes 35-54 in number, in one layer, between vitellaria, anterior to ovary. Diameter of testes 0.04-0.05 mm. Vas deferens forming mass of coils in mid-field. Cirrus-pouch 0.289-0.340 mm. long, reaching to the middle of segment. Cirrus straight, 0.10 mm. long when protruded. Vagina anterior to cirrus-pouch, crossing cirrus-pouch near middle. Sphincter vaginae weak, 0.008 mm. thick. Lobes of ovary retort-shaped with smooth outlines. Vitelline follicles small, not compact. Uterus when fully developed with 9-14 lateral pouches on either side. Embryos about 0.019-0.021 mm. in diameter, second egg membrane 0.036-0.046 mm., outer membrane 0.038-0.06 mm.

Habitat: In stomach (probably by post-mortem wandering) and intestine of host.

Host	Locality	Collector	Authority
<i>Coregonus nigripinnis</i>	Lake Michigan near Charlevoix	H. B. Ward	La Rue
<i>C. prognathus</i>	As above	H. B. Ward	La Rue
<i>C. artedi</i>	As above	H. B. Ward	La Rue

Type: Alcoholics No. Ch. 7c, Ch. 2c, and an unnumbered bottle in Doctor H. B. Ward's collection, from *Coregonus nigripinnis*, *C. prognathus*, and *C. artedi*. Type locality, Lake Michigan, near Charlevoix.



Benedict (1900:355-365) described some cestodes which had been collected by Dr. H. B. Ward while engaged in a biological investigation of Lake Michigan under the auspices of the Michigan Fish Commission during the summer of 1894. The hosts were *Coregonus nigripinnis*, *C. prognathus*, and *C. artedi*. Benedict who had for comparison some specimens identified by Zschokke as *Taenia ocellata* Rud. (probably *P. fallax* La Rue) thought his material and Zschokke's specifically identical. He, however, called attention to the fact that Zschokke's specimens had been nearly dried out in transit and consequently were almost ruined for study. Accepting Kraemer's statement that *Taenia filicollis* Rud. and *T. ocellata* Rud. were identical he used the name *Proteocephalus filicollis* (Rud.) to designate his form. Later he discovered that the name *Taenia ocellata* Rud. had page precedence in the original paper by Rudolphi (1803) and in a foot-note he called attention to the fact that the name *Proteocephalus ocellata* (Rud.), mis-spelling for *ocellatus*, should be used to designate the form. La Rue (1911:477-478) distinguished this species from *P. filicollis* and described it as a new species *P. exiguus*.

Careful examination of prepared specimens from some of the same lots used by Benedict in his research and a study of one of his slides together with a comparison of these with specimens which Zschokke had sent to Dr. H. B. Ward under the name of *Taenia ocellata*—(now No. 09.9 in Professor Ward's collection)—has convinced the writer that Benedict's species is a new one. La Rue (1911) proposed for it the name *Proteocephalus exiguus* La Rue by reason of the small size of the individuals. Benedict worked out the morphology of the form quite correctly and probably would have given due weight to the difference between his own and Zschokke's specimens had the latter been in good condition.

This species is based upon the work of Benedict (1900:355-365) and upon a further examination of, and collection of, data from certain lots of alcoholic material in Dr. H. B. Ward's collection from which Benedict secured his specimens for study. These bottles bear the labels "Long-jaw, stomach. Charlevoix Jy. 16, '94". "Ch. 7 c, Cestodes, Etc. Stomach Black-fin Charlevoix, Jy. 16, '94." "Ch. 3 c, cestodes. *Coregonus Artedi* Jy. 12, '94". Slides have been prepared from the first two lots.

The specimens which were examined carefully by the writer ranged in length from 9-10-15 mm. Benedict found the length to vary from 12-16-25 and one specimen only attained the length of 38 mm. This one case seemed to have been due to an extreme attenuation for the neck was 7 mm. long. This attenuation may have been caused by the method

of killing. The maximum breadth found by the writer varied from 0.425-0.595-0.646 mm. while Benedict records a maximum of 0.8 mm. The globular head according to Benedict is 0.120 mm. broad. The writer found it to be 0.148-0.160-0.170 mm. broad. The suckers placed just above the broadest zone are directed slightly anteriorly. They are 0.069-0.085 mm. long by 0.058 mm. broad with an opening of 0.042-0.048 mm. by 0.027-0.032 mm. Benedict states that the sucker is 0.040 mm. in diameter, but it seems that he must mean the diameter of the opening and not the diameter over the whole sucker. A fifth sucker is present, 0.037-0.048 mm. in diameter. This from *toto* preparations is apparently a true sucker. Benedict says it has the "same structure and musculature that the four large suckers possess." His drawing of the head is reproduced (Fig. 138).

The neck measures 2-4 mm. in length by 0.110-0.120 mm. broad. Benedict found the neck to be 5-10 mm. long by 0.10-0.20 mm. broad. The neck passes over into the first proglottids almost imperceptibly. The first proglottids are longer than broad or nearly quadrate. These very immature proglottids are few in number. The anlage of the genital organs appear very early and in proglottids a little further back mature sexual organs appear. Mature proglottids are longer than broad and are few in number. Ripe proglottids are longer than broad. Three of these measured 0.935 by 0.595 mm., 0.680 by 0.560 mm., 1.190 by 0.460 mm. Ripe proglottids are considerably larger than the mature. The increase in length, breadth and thickness is rapid. The longest proglottid in the strobila is usually the last one and sometimes also it is the broadest. Three terminal proglottids measured 1.190 by 0.646 mm., 0.714 by 0.51 mm., 1.50 by 0.40 mm., the length being stated first. The end proglottid is variable in form and functional. It usually tapers to a blunt point at its posterior end where the excretory pore is situated. The segmentation is not evident. The angles at the ends of the proglottids are scarcely marked and the intersegmental furrows are shallow. The total number of proglottids in a strobila is small, 10-12-14-15-20. Benedict found one specimen with 40 segments.

Benedict's findings on points of histology are probably correct and have not been checked over. The common genital sinus is situated near the middle of the margin of the proglottid, usually slightly anterior thereto. It alternates irregularly.

The testes (Fig. 50) are 37-50-54 in number, 35-50 according to Benedict. They measure 0.040-0.045-0.050 mm. in diameter. The testes lie in a single layer between the vitellaria and anterior to the ovary. In *toto* mounts the writer could not make out with certainty the coils of the vas deferens yet they seemed to lie in the middle of the

proglottid near the dorsal wall. Benedict figures the vas deferens as forming a coil extending beyond the middle of the segment. The cirrus-pouch (Figs. 50, 51, 52) is elongated, slightly broader near its inner extremity and slightly constricted near the middle. It reaches the middle of the segment or even beyond that point in mature proglottids. Its length increases with the maturity of the segment. The following measurements of its length were taken from successive proglottids, 0.289, 0.296, 0.313, 0.330, 0.341 mm. the last being the maximum length found. The unprotruded cirrus is straight. The writer has not seen it evaginated. According to Benedict the evaginated cirrus extends 0.10 mm. from the male opening. The ductus ejaculatorius is straight.

The vagina (Figs. 50, 51, 52) opens into the common genital sinus and it always lies anterior to the cirrus-pouch. In a single proglottid the vagina was found posterior to the cirrus-pouch. This is probably to be considered as an abnormality or a very rare variation. A weak sphincter vaginae occurs a short distance from the vaginal opening. This sphincter is 0.008 mm. thick and is circular in cross section (Benedict). As Benedict has described it, the vagina extends straight in for a short distance then it "bends backward and inward passing under the middle of the cirrus-sac". The ovary very much resembles that of *P. fallax* (Kraemer's *Taenia ocellata*) in shape. The lobes are thick and solid. Benedict's comparison of their shape to that of a retort is excellent. The ovary is early decadent. The relations of the organs of the interovarial space are typical of the genus as Benedict has described them. The vitellaria are follicular. The follicles are not large nor are they closely packed. They too are decadent early. The uterus (Figs. 51, 52) in ripe proglottids consists of a median tube and 9-14 lateral pouches on either side. These pouches occupy the ventral part of the segment while the testes are dorsal. "The eggs which are found in the uterus have a diameter of 0.02 mm." (Benedict). Measurements by the writer gave a range of 0.019-0.021 mm. for the embryo and 0.036-0.046 mm. for the second membrane. The outer membrane measures 0.038-0.060 mm. The second membrane is thick and granular while the outer membrane in uterine eggs is thick and hyaline.

This species somewhat resembles *P. pusillus* Ward but is differentiated from that species by the smaller size of its head, by its very much smaller suckers and smaller sucker openings. This species has a much longer neck than has *P. pusillus*. The character of the segmentation of the two worms is utterly different being very evident in *P. pusillus*, with deep constrictions between proglottids. In *P. exiguus* segmentation is not evident. The number of proglottids in *P. pusillus* is greater



than in *P. exiguus*. The mass of coils of the vas deferens in *P. pusillus* is much smaller than in *P. exiguus* and it lies almost wholly anterior to the cirrus-pouch while in *P. exiguus* it lies more nearly at the end of the cirrus-pouch. The testes are more numerous in *P. pusillus* and the cirrus-pouch is much shorter than in *P. exiguus*. The lobes of the ovaries in *P. pusillus* are bent strongly posteriad while such a condition is never so marked in *P. exiguus*. The proportions of the proglottids are greatly different.

*P. exiguus* closely resembles *P. fallax* La Rue. It differs from that species in having a smaller head, smaller suckers, a smaller fifth sucker, a shorter neck, fewer and smaller proglottids, more testes, a shorter cirrus when evaginated, and a greater number of lateral uterine out-pocketings. The embryos of *P. exiguus* are smaller than in *P. fallax*. The differences are of such a character and of such a constancy as to be of specific importance. This species resembles *P. agonis* Barbieri even more than it does *P. fallax* except that *P. agonis* has no well developed fifth sucker. In total length and in the size of the proglottids *P. exiguus* is the larger. *P. exiguus* has more uterine pouches and fewer but larger testes than has *P. agonis*. Unfortunately Barbieri's description fails in some particulars, nevertheless sufficient data are given to establish the difference between the two species. *P. exiguus* resembles *P. dubius* La Rue but its head, its suckers, its proglottids, and its cirrus-pouch are smaller. These two species have about the same number of testes. The embryo of *P. dubius* is much larger than that of *P. exiguus*. *P. exiguus* differs radically from *P. ambiguus* and *P. esocis* in the possession of a fifth sucker. Other points of difference are also to be found. *P. exiguus* is smaller than other North American species of *Proteocephalus*.

#### PROTEOCEPHALUS PUSILLUS Ward

[Figs. 2-4, 53-55]

1910: *Proteocephalus pusillus* Ward, 1910:1185-1187

1911: *Proteocephalus pusillus* La Rue, 1911:475

Specific Diagnosis: Characters of the genus. Cestodes small, length 30-50 mm. Maximum breadth 0.350 mm. Proglottids few. Segmentation distinct. Head spheroidal, frequently much contracted, breadth about 0.300 mm., length about 0.260 mm. Four suckers placed at broadest zone of head. Suckers deep, 0.140 mm. long by 0.110 mm. broad. Fifth sucker well developed, muscular, 0.060 mm. in diameter. Neck 1.0-1.5 mm. long by 0.21 mm. broad. First proglottids broader than long, breadth of same 0.090 mm. Mature proglottids longer than

broad. Ripe proglottids much longer than broad. Length of same 0.84-1.4 mm., breadth 0.18-0.35 mm. End-proglottid present and fertile.

Genital sinus marginal, irregularly alternating, situated at end of first  $\frac{1}{3}$ - $\frac{2}{5}$  of proglottid. Vagina usually anterior and dorsal to cirrus-pouch, rarely posterior. Testes 44-60-70 in number, arranged in two layers between vitellaria. Length of same 0.06-0.096 mm., breadth 0.04-0.05 mm. Vas deferens a small mass of coils anterior to cirrus-pouch. Cirrus-pouch 0.095-0.106 mm. long by 0.053-0.060 mm. broad, reaching  $\frac{1}{3}$ - $\frac{1}{4}$  across the proglottid breadth. Ductus ejaculatorius forming one or two coils in cirrus-pouch. Cirrus short and straight. Vagina never crossing cirrus-pouch. Sphincter vaginae and receptaculum seminis not seen. Ovary bilobed, posterior. Lobes short, thick, free ends of same frequently pressed posteriad and together. Vitellaria sparse, follicles small. Uterus with 10-14-16 lateral pouches on either side. Eggs not observed.

Habitat: Intestine and esophagus of *Salmo sebago* Girard (type host), Sebago Lake, Me. (type locality); intestine and pyloric coeca of *Cristivomer namaycush* Walbaum (?), Lake Temagami, Ontario.

Type: Material in bottles 15, 16, 42, in Professor Ward's collection from Sebago Lake, Me., summer of 1907, and slides from this material.

Ward (1910:1185-1187) first described this species which he had found in the Sebago salmon. Ward's description follows.

"*Proteocephalus pusillus* nov. spec.—Adult cestode with short strobila, measuring only 30 to 50 mm. in length. Proglottids scanty, segmentation distinct. Head much contracted. Neck 1 to 1.5 mm. long by 0.21 mm. broad. First proglottids 0.09 mm. broad changing gradually until in mature proglottids the length greatly exceeds the breadth. Ripe proglottids measure 0.84 to 1.4 mm. long by 0.18 to 0.35 mm. broad. Terminal proglottids present and fertile. Sexual organs typical for *Proteocephalus*; uterus median, with 10 to 14 lateral outpocketings on either side. Testes numerous, within vitellaria. Genital pore lateral, one-third to two-fifths of length of proglottid from anterior margin of same. Ovaries bilobed, median isthmus indistinct, anteroposterior diameter nearly equal to breadth of both lobes. Only a few specimens obtained from a single host species, *Salmo sebago*.

"This species approaches most nearly to *P. ocellata* and *P. percae* among known species. Unlike the new species, however, both of these older forms have a fifth sucker, a few lateral uterine outpocketings, a longer neck, differently shaped ovaries, and markedly different proglottids.

"In specimens with developed proglottids the head was so much contracted or distorted that any special description would be of little value. One could easily observe the general features characteristic of the genus. There was no well developed terminal or fifth sucker, and the end organ, which is known to

replace it in many forms of this genus, was inconspicuously developed, if present. Personally, I incline to the view that on more careful examination this structure will be found in all species, even those in which its absence has been made a matter of record. Accordingly, not much weight can be put in its presence or absence in any individual.

"Three plerocercoid larvae or young cestodes were found in company with *Proteocephalus pusillus*, which I regard as young forms of this species. The largest came from the salmon which was most heavily infected with this cestode parasite. It was 3.15 mm. long and had begun to assume clearly the appearance of an immature cestode. The head measured 0.3 mm. wide by 0.26 mm. long, and the suckers 0.14 mm. in length by 0.11 mm. in width. The neck was slightly narrower than the head, but was not clearly set off from the body, which was very uniform in diameter and measured 0.25 mm. in average width. The posterior end of the body was swollen into a rounded knob about 0.35 mm. broad and of approximately the same length. This feature was evidently produced by a powerful contraction of the terminal region of the body. In and near it one could see very indistinct indications of proglottid formation. In form, size, and general aspect this young cestode was in full agreement with the anterior regions of the mature cestodes of this species with which it was associated. The head, which was not contracted, showed on careful study the delicate outline of a rudimentary end organ. While such a structure was not demonstrated in the mature individuals described above, one can say positively that if present it could not have been seen owing to the greatly contracted condition of the adult scolices. I believe that its presence will be demonstrated in more favorable specimens. The complete agreement of this largest larva with the mature specimens in all other features compels me to regard both as different stages in the development of the same species.

"The other larvae were still in early stages of development and probably had been ingested by the salmon at a very recent date. Their relationship is not so clear in all respects, and yet I do not hesitate to associate with the new species of *Proteocephalus* a plerocercoid or young cestode obtained from the same host as the adult worms and the older larva just described. The head is broadly conical, without furrows, and measures 0.3 mm. in breadth. The suckers measure 60 to 74  $\mu$  in diameter. There is no rostellum or fifth sucker to be found, while the end organ is so poorly developed as to be visible with difficulty and only under the most favorable circumstances. The neck is nearly as broad as the head. In general appearance this larva resembles the adult cestode and the older larva previously described. With some reserve one may also assign to this species a single plerocercus taken from another specimen of *Salmo sebago*. The head, which measures only 150  $\mu$  in breadth, is shaped like that of the young cestode and like it is without rostellum or fifth sucker, while the end organ is difficult to demonstrate. Neither furrows nor ridges are seen on the larva, which has a total length of 1.14 mm. The sucker measures only 30 to 45  $\mu$  in diameter. The neck is slightly narrower than the head. This form certainly belongs to the genus *Proteocephalus* and probably to the species already described."



La Rue (1911:475) listed this form among other *Proteocephalus* species. Dr. H. B. Ward has very kindly loaned the writer his specimens for study. More preparations have been made and from them the writer has been able to secure additional data on this species.

The type material in bottles 15, 16 and 42 was taken from the intestine and oesophagus of *Salmo sebago* Girard, Sebago Lake, Me. Jy. 27 and Aug. 6, 1907. Other specimens which the writer has assigned to this same species were taken by Dr. H. B. Ward from two specimens of *Cristivomer namaycush* Walbaum (?), Lake Temagami, Ontario, in August, 1911. These last are described separately.

This is one of the smaller species of *Proteocephalus*. The observed length is from 30-50 mm. for specimens which have ripe proglottids. Proglottids are few in number and the segmentation is distinct. The head is spheroidal but in many cases it is so greatly contracted that its structure can not be determined. The head measures 0.300 mm. broad by about 0.260 mm. long. The four suckers measure about 0.140 mm. long by 0.110 mm. broad. The sucker cavity is quite deep. At the apex of the head (Figs. 2, 3, 4) is a fairly well developed fifth sucker which in well stained specimens shows an evident musculature and a cavity. Ward (1910) reported only an end organ or vestigial fifth sucker instead of a fifth sucker. When his specimen was restrained and mounted it showed a well formed fifth sucker. Characteristic fifth suckers measure about 0.060 mm. in diameter. The neck is 1-1.5 mm. long by about 0.21 mm. broad. It passes over quickly into the first proglottids which are broader than long. Their breadth is about 0.090 mm. The proglottids rapidly become quadrate or even longer than broad. Ripe proglottids measure 0.84-1.4 mm. long by 0.18-0.35 mm. broad. An end-proglottid is usually present and fertile.

The common genital sinus is marginal, situated at the end of the first  $\frac{1}{3}$ - $\frac{2}{5}$  of the proglottid. Its position alternates irregularly. The testes (Figs. 54, 55) number 44-60-70. Since these lie in two layers the figure does not show all of them. In less mature proglottids where the testes are much smaller and more distinct they can be counted more readily. The testes measure 0.06-0.072-0.096 mm. long by 0.040-0.050 mm. broad. The vas deferens (Figs. 53, 54, 55) forms a small mass of coils in the middle of the proglottid. The larger part of the mass is anterior to the cirrus-pouch, a condition not usually met with in this genus. The cirrus-pouch which is rather heavy reaches  $\frac{1}{4}$ - $\frac{1}{3}$  across the proglottid breadth. Its length is 0.095-0.106 mm. and its breadth 0.053-0.060 mm. The ductus ejaculatorius forms a coil or two within the cirrus-pouch before passing over into the short straight cirrus which has not been seen protruded. On account of a lack of suffi-

cient material but very few sections have been made and these were too poor to yield much valuable data.

The vagina (Figs. 54, 55) usually opens anterior and dorsal to the cirrus-pouch but rarely (Fig. 53) it is posterior to the same. The number of proglottids examined have been too few to establish whether the posterior position of the vagina is normal. Even when in the anterior situation the vagina does not cross the cirrus-pouch. From its opening it makes a long curve toward the middle of the proglottid which it reaches at a point posterior to the inner end of the cirrus-pouch. The vagina is dorsal to the uterus. A vaginal sphincter could not be demonstrated, and if present it must be very weak. The presence of a receptaculum seminis has not been demonstrated. The bilobed ovary (Figs. 53, 54, 55) is peculiar in that the lobes which are short and very thick are pressed closely together. This is a condition not yet found regularly in any other species of the genus altho Nufer (1905) found it in *P. macrocephalus*. In transverse sections the thickness and compactness of the ovary are noted at once. The vitellaria are sparse, the follicles small. The ducts of the interovarial space have not been thoroly investigated. An oötype and an oöcapt are present.

In ripe proglottids the uterus (Fig. 53) shows 10-14-16 lateral out-pocketings on either side. No uterine pores have been seen. The eggs have not been observed.

Other specimens which the writer has provisionally assigned to this species were taken by Dr. H. B. Ward from the pyloric and intestinal regions of *Cristivomer namaycush* Walbaum (?), Lake Temagami, Ontario, August, 1910. It seems that the determination of the host must remain somewhat in doubt for there was no attempt at the identification of the fish when it was caught and it was not preserved. The identification was made from the memory of the appearance of the fish after the return of the expedition. Both Professor Reighard and Professor Ward when questioned by the writer thought there could be little doubt of the determination. These specimens bear the lot numbers T1p, T1j, T2h, and T2p in Dr. H. B. Ward's collection.

The specimens are small, measuring up to 20-30 mm. long. No specimens have ripe proglottids. When the worm is fully mature it is perhaps considerably longer. Measurements of a number of specimens yielded the following data: Average breadth of seven heads 0.284 mm., maximum breadth of same 0.340 mm., minimum 0.244 mm.; average length of six heads 0.177 mm., maximum length of same 0.238 mm., minimum 0.133 mm.; average length of seventeen suckers 0.134 mm., maximum length of same 0.179 mm., minimum 0.106 mm.; average breadth of thirteen suckers 0.108 mm., maximum breadth of same 0.127 mm.,

minimum 0.096 mm.; sucker opening 0.058-0.080 mm.; diameter of fifth sucker about 0.060 mm. Average length of six necks 1.49 mm., maximum length 1.70 mm., minimum 1.02 mm.; neck narrow, up to 0.135 mm. The proglottids are few, numbering about 30-40. First proglottids are broader than long, or quadrate, length soon exceeds breadth, and mature proglottids are longer than broad measuring up to 0.56-0.68 mm. long by 0.24-0.265 mm. broad. The maximum breadth of 0.340 mm. was observed in a proglottid measuring 0.357 mm. long by 0.340 mm. broad. Segmentation is very distinct.

The genital pore is near the middle, usually anterior thereto but sometimes posterior. The vagina lies anterior to the cirrus-pouch. There are about 44-66 testes and these measure about 0.159 by 0.180 mm. in diameter. They form two irregular layers in the region bounded by the vitellaria and ovary. In many proglottids of this lot the testes are not as fully developed as in the proglottids of specimens from *Salmo sebago*. This condition facilitates the counting of the testes. The coils of the vas deferens form a small mass situated for the most part anterior to the cirrus-pouch. Within the cirrus-pouch the ductus ejaculatorius forms a single coil and then it passes over into the small cirrus. The cirrus-pouch usually extends to the middle of the proglottid or nearly thereto. It has a length of about 0.111-0.150 mm. The average length of eight pouches was 0.133 mm. In breadth the cirrus-pouch measures 0.053-0.070 mm. The lobes of the ovary are thick and are bent back until they nearly meet in the median line. Vitellaria are sparse. A fully developed uterus has not been observed. Of the drawings representing *P. pusillus*, figures 2, 4, and 55 were made from specimens which came from *Cristivomer namaycush*. All the other drawings of this species were made from specimens taken from *Salmo sebago*.

In general these two forms agree very well but there are two points of minor disagreement. These are in regard to the length of the cirrus-pouch and the size of the suckers. As to the former the difference in length is but a matter of a few micra and this perhaps may be explained by the fact that the proglottids are in different states of contraction. As for the other point of difference it may be stated that in the specimens taken from *Cristivomer namaycush* the suckers are on the average about the size of the suckers of the typical *P. pusillus* but in one or two cases observed the length and breadth of the sucker is appreciably larger. It is to be remembered that the measurements of the suckers of the typical *P. pusillus* are based on a single head. Consequently the range of size of suckers in that species has not been determined. Tho no ripe proglottids were present in the material from *Cristivomer na-*



*maycush* and consequently some of the best diagnostic features could not be determined it seems best to consider these forms identical.

*Proteocephalus pusillus* Ward is closely allied to *P. exiguus* La Rue but is differentiated from that species by its larger head, larger suckers, and larger sucker openings. The measurements of proglottids of the two species are much alike. However, the type of segmentation is very dissimilar. In the reproductive organs *P. pusillus* varies from *P. exiguus* in having more numerous and larger testes. The testes of *P. pusillus* lie in two layers while in *P. exiguus* they are in one layer. The cirrus-pouch of *P. exiguus* is much longer than that of *P. pusillus*. The ovaries of the two species are very different. In the one species the lobes are slightly arched while in the other the lobes are bent nearly together. The lateral uterine pouches of *P. exiguus* are larger and scarcely as numerous as in *P. pusillus*. *P. pusillus* somewhat resembles *P. fallax* La Rue but it is smaller. It has a larger head and suckers, more numerous and larger testes, a much shorter cirrus-pouch, and more numerous uterine outpocketings than *P. fallax*. The ovaries of the two species are very different.

*P. pusillus* differs from *P. agonis* Barbieri in having a fifth sucker. Moreover *P. pusillus* is a larger form than *P. agonis*. *P. agonis* has smaller and more numerous testes than *P. pusillus*, and also fewer uterine outpocketings. *P. pusillus* differs radically in size and proportions from *P. percae* (O. F. Müller). *P. pusillus* differs from *P. esocis* (Schneider) in having a larger head, larger suckers, in possessing a fifth sucker, and a shorter neck. The proportions of the segments are different. The length of the cirrus-pouch and the ratio of its length to the proglottid breadth differ greatly in the two species. The character of the segmentation is very unlike. There is very little probability that *P. pusillus* is the same as *P. salvelini* (Linton). *P. salvelini* has no fifth sucker. Its head, suckers, and cirrus-pouch are larger than those of *P. pusillus*. Linton's description of *P. salvelini* does not furnish many characters for determination and his drawing of the proglottid is so indistinct that it cannot be relied upon as a source of data.

## PROTEOCEPHALUS PINGUIS La Rue

[Figs. 29-32, 35, 36, 88-93]

1911: *Proteocephalus pinguis* La Rue, 1911:478.

Specific Diagnosis: Characters of genus. Strobila short and slender. Observed length up to 90 mm. Maximum breadth 1.24 mm. Neck 3-7 mm. long by 0.20-0.25 mm. broad. Proglottids, first in chain very short, 0.05 mm. long by 0.25 mm. broad. Mature and ripe proglottids nearly quadrate or in a few ripe proglottids length exceeding the breadth, 0.595 by 0.595 mm. up to 0.730 mm. long by 0.595 mm. broad. End-proglottid present and functional. Segmentation not very distinct. Intersegmental furrows shallow. Head conical, flattened dorso-ventrally, without furrows, presenting great variations in shape. Breadth of head about 0.33 mm., thickness 0.22 mm., length 0.20-0.25 mm. Suckers cup-shaped, deep, muscular. Diameter of suckers 0.095-0.105 mm., of aperture of sucker 0.06-0.07 mm. Diameter of fifth sucker 0.05-0.075 mm.

Common genital sinus irregularly alternating, situate at or near middle of lateral margin of proglottid. Testes ovoidal, 0.05 mm. long by 0.04-0.05 mm. broad, 54-70 in number, in a single layer taking up field between vitellaria anterior to ovary. Ductus ejaculatorius nearly straight. Cirrus well muscled, straight, length when protruded 0.07-0.08 mm. by 0.02-0.025 mm. broad. Cirrus-pouch short, stout, 0.13-0.14 mm. long by 0.05-0.06 mm. broad. Ratio of length of cirrus-pouch to breadth of proglottid 1:3 or 1:4. Vagina anterior, but vaginal opening always dorsal to cirrus-pouch. Vagina crossing inner end of cirrus-sheath. Sphincter vaginae small. Receptaculum seminis small, situate anterior to ovary. Uterus, when fully developed, with 10-14 lateral pouches on either side. Ventral uterine pores 2-3 in number. Embryos 0.016-0.018 mm. in diameter.

Habitat: In intestine of host.

Host	Locality	Collector	Authority
<i>Esox reticulatus</i> Le Sueur	Sebago Lake, Maine	H. B. Ward	La Rue (the present paper)
<i>Esox lucius</i> Linn.	Walnut Lake, Mich.	T. L. Hankinson	La Rue (the present paper)
<i>Esox lucius</i> Linn.	Lake Geneva, Wis.	A. J. Coats	La Rue (the present paper)

Type: Alcoholics in Dr. H. B. Ward's Sebago Lake collection Nos. 4, 6, 7, 8, 9, 107. Slides of same. The material was collected by

Dr. H. B. Ward from *Esox reticulatus* Le Sueur (type host); Sebago Lake, Maine (type locality).

Co-type: Alcoholics No. TLH413 in Dr. H. B. Ward's collection, from *Esox lucius* Linn., Walnut Lake, Michigan, and slides of the same.

Autotype: Alcoholics No. 10.35 in collection Dr. H. B. Ward from *Esox lucius* Linn., Lake Geneva, Wisconsin.

Leidy (1888:169 and 1890:417) described some specimens of cestodes from *Esox reticulatus*. The two specific names which he proposed for them the writer considers to be synonyms and has included under the one name, *Proteocephalus nematosoma* (Leidy). Leidy's specimens were considerably larger than the specimens of *P. pinguis* and apparently are not the same. A more complete discussion of Leidy's species occurs later in the article. La Rue (1911:478) briefly characterized this species and proposed for it the name *Proteocephalus pinguis*.

This study is based, for the most part, upon specimens collected by Dr. H. B. Ward from the intestines of *Esox reticulatus* Le Sueur at Sebago Lake, Maine, while engaged in an investigation of that lake for the U. S. Bureau of Fisheries, in the summer of 1907. Portions of the study are also based upon specimens secured by Prof. T. L. Hankinson from *Esox lucius* Linn, in the course of a biological investigation of Walnut Lake, Mich., during the summer of 1906. This last material was referred to in a former paper, La Rue (1909:25), as "A new species, which I shall describe in detail later——". It bears the number TLH413 in Professor Ward's collection. Dr. H. B. Ward examined six specimens of *Esox reticulatus* Le Sueur while at Sebago Lake. These six fish yielded sixteen entire Proteocephalids and pieces as follows: No. 4, 1 head+2 pieces; No. 6, 2 heads+2-3 pieces; No. 7, 1 head+2 pieces; No. 8, 11 heads+2 pieces; No. 9, 1 head; No. 107, 5 heads, 1 young cestode+10 large pieces. In many instances the specimens reported as heads were complete worms while in others the end proglottid and part of the strobila were missing. Thus the infection of Sebago Lake hosts was light. Hankinson's material in bottle No. 413 from *Esox lucius* of Walnut Lake was probably from a single host. It contained 60-70 specimens of *P. pinguis*. A bottle, No. 10.35 in Dr. H. B. Ward's collection, bearing the label "from stomach and intestine of a 'pickerel,' Lake Geneva, Wisconsin, Jy. 1, 1904. A. J. Coats, collector", contained 5 or 6 complete specimens of *P. pinguis* La Rue and several pieces of the same species. Replying to a letter of inquiry Prof. George Wagner of the University of Wisconsin states that only one species of pickerel, the *Esox lucius*, is found in Lake Geneva, Wisconsin. The data on this species were obtained from specimens cleared and examined in



glycerine, from specimens stained and mounted in toto and from transverse and frontal sections.

These cestodes are small and slender (Fig. 32). The largest specimen from the Sebago Lake material measured 90 mm. long by 1.24 mm. in maximum breadth. The longest specimen from the Walnut Lake host measured 66 mm. long by 1.0 mm. in maximum breadth. The strobila of a 50 mm. specimen is made up of an unsegmented neck 3-7 mm. long by 0.20-0.25 mm. broad followed by 300 proglottids. The youngest proglottids measure about 0.050 mm. long by 0.250 mm. broad. Further along in the chain these increase in length and breadth until in mature and ripe proglottids the length and breadth are about equal. Measurements of several ripe proglottids are as follows, the length in millimeters being stated first: 0.595 by 0.595, 0.680 by 0.680, 0.595 by 0.663, 0.730 by 0.595 mm. In transection the proglottids are elliptical.

A typical functional end-proglottid with a rounded posterior end is present. The segmentation is not very plain, for the inter-segmental furrows are not deep and the corners of the proglottids do not project. The lateral margins are rounded and smooth. The head (Figs. 29-32, 35, 36) is a cone-shaped structure somewhat flattened dorso-ventrally. It is not marked by folds or furrows. Its breadth is about 0.33 mm., its thickness about 0.22 mm., its length about 0.20-0.25 mm. In extreme cases the head may attain a breadth of 0.45 mm. This extreme breadth is due to a contraction of the longitudinal muscles of the head and neck. A collection of these specimens shows heads of very different states of contraction. The head bears on its broadest part four deep cup-shaped muscular suckers which are directed forward and outward. On its apex the head bears a well formed muscular fifth sucker. The diameter of the suckers ranges from 0.095-0.105 mm., while the diameter of the aperture varies from 0.06-0.07 mm. The fifth sucker measures 0.05-0.075 mm. in diameter. Altho its cavity is quite shallow it has the appearance of being functional for it possesses a typical musculature (Fig. 93).

The cuticula and musculature have not been found to differ in their essential features from those of other members of the genus. The nervous system in the head is much like that of *Ophiotaenia filaroides*. A ganglionic mass is located at the level of the suckers (Fig. 93). Two main lateral nerve trunks extend throughout the length of the strobila. No accessory nerve trunks were observed.

The excretory system in the head is made up of four main longitudinal canals which at various levels receive many anastomosing coiled vessels which pass through the tissues of the scolex and neck in every direction. In the strobila there are two pairs of lateral excretory vessels, ventral and dorsal respectively. These lie within the medullary

parenchyma. The dorsal vessel passes dorsad and the ventral vessel ventrad to the cirrus-pouch and vagina. In diameter the ventral vessel greatly exceeds the dorsal and its lining membrane is thin while the membrane lining the dorsal vessel is thick. A posterior excretory commissure in each proglottid could not be found. Numerous secondary excretory openings which are connected with the ventral vessel and less frequently with the dorsal vessel have been seen. The drawing (Fig. 91) shows rather an extraordinary case in that the duct is larger and more extensive in its connections than is usual. In the end-proglottid the four main excretory ducts discharge to the exterior by a common pore. A bladder could not be seen.

The common genital sinus is marginal, situated at or near the middle of the proglottid. While the vagina lies anterior to the cirrus-pouch, the opening of the vagina, without exception, is dorsal to the opening of the cirrus (Figs. 88, 90). There is no genital papilla. The testes (Fig. 92) are numerous, 54-70. These are in a single layer in the medullary parenchyma, occupying nearly the entire field between the vitellaria anterior to the ovary. The testes measure as much as 0.05 mm. long by 0.04-0.05 mm. broad. The vasa efferentia (Fig. 90) form a network of fine anastomosing tubules just dorsal to the testes and within the medullary parenchyma. The main branches of the vasa efferentia unite to form the larger vas deferens. The junction occurs at a point near the median line about one-fourth the distance from the anterior to the posterior end of the segment. From this point of juncture the vas deferens forms a mass of coils extending to the cirrus-pouch. These coils function as a vesicula seminalis. When the vas deferens enters the cirrus-pouch it receives some additional glandular elements, the prostate cells. This part of the vas deferens is called the ductus ejaculatorius. The ductus in this species is very nearly straight. The cirrus which is a continuation of the ductus ejaculatorius has a heavier musculature than is present in any other part of this canal. The cirrus lies in the pouch as an almost straight organ. When protruded it measures 0.07-0.08 mm. long by 0.02-0.025 mm. broad. The cirrus-pouch is elongated oval in outline. It is short and stout, being 0.13-0.14 mm. long by 0.05-0.06 mm. broad. The ratio of its length to the proglottid breadth is 1:4 to 1:3.

The vaginal pore opens into the genital sinus just dorsal to the cirrus-pouch tho the greater part of the initial part of the vagina itself lies anterior to the pouch. A small sphincter vaginae is situated near the opening. In its course to the mid-field the vagina crosses the inner end of the cirrus-sheath. When passing posteriad to enter the inter-ovarial space the vagina is straight, not sinuous or coiled. Just anterior to the ovary the vagina dilates slightly to form a receptaculum seminis. The relations of the vagina are shown in figures 88, 90, and 92. The ovary is bi-lobed. The lobes (Fig. 92) are elongated oval and smooth in

outline. The vitellaria are typical of the genus. The uterus is formed of a median ventral-lying tube which extends nearly the full length of the proglottid. From this tube, by the process described for *Ophiotaenia filaroides*, lateral outpocketings arise. These lateral pouches (Fig. 92) number 10-14 on either side. As the pouches become filled with eggs the outlines of some of them are nearly obliterated. Yet in all but the ripest proglottids the full number is visible. Sections through mature and ripening proglottids show the pouches in all stages of development. Sections also reveal the ventral diverticula which finally come to open on the surface. Such diverticula were described in an earlier paper (La Rue 1909:36) for *Ophiotaenia filaroides* and their presence in other species was at that time noted. In *P. pinguis* the number of ventral diverticula is greater than Gui. Schneider (1905) reported in *P. macrocephalus*, *P. percae*, *P. esocis*, and *P. ambiguus* but smaller than the number reported by the writer for *O. filaroides*. A drawing (Fig. 89) of a frontal section just below the cuticula shows two of these openings. In such sections the openings, usually two or three, and the tubes leading up to them could be readily traced. A specimen cleared in glycerine showed these openings beautifully. The actual count of openings on 25 consecutive proglottids of this specimen is as follows: 1, 2, 3, 2, 2, 2, 1, 1, 2, 3, 2, 2, 2, 2, 3, 2, 4, 3, 2, 4, 2, 3, 3, 3. The uterine eggs were observed only in preserved condition. The outer mucilaginous envelope could not be seen. The embryos measured 0.016-0.018 mm.

*Proteocephalus pinguis* La Rue is a much larger form than *P. esocis* (Gui. Schneider). It has a fifth sucker which the latter lacks. It differs from that species in having a larger head, larger suckers, larger proglottids, more testes and a relatively shorter cirrus-pouch. *P. pinguis* differs from *P. pusillus* Ward, a species occurring in the same locality, in the possession of a larger head, larger suckers, larger proglottids which have proportions different from those of *P. pusillus*. Moreover, the segmentation is of a different character and the relative lengths of the cirrus-pouches in the two worms are very different. *P. pinguis* differs very much from *P. exiguus* La Rue in size, in the proportions of the proglottids, in the size of the head and of the suckers, in the relative length of the cirrus-pouch, in the character of the uterine pouches and in the size of the embryos.

*P. pinguis* differs from *P. macrocephalus* (Creplin) in having a fifth sucker, in being considerably smaller, in the relative length of the cirrus-pouch, in the number of testes, and in the size of the embryos. *P. pinguis* is smaller than *P. ambloplitis* (Leidy), *P. singularis* La Rue and *P. perplexus* La Rue. There is also a difference in the size and character of the head and suckers. It is further differentiated from



those species by the presence of a functional fifth sucker which those species lack. *P. pinguis* is quite different from the European forms which have fifth suckers. These are *P. percae* (O. F. Müller), *P. fallax* La Rue, *P. dubius* La Rue, *P. cernuae* (Gmelin), *P. longicollis* (Rud.). It differs from them in size of body, size of suckers and of proglottids, in the relative length of cirrus-pouch, in the size of the embryos and in the number of testes.

### PROTEOCEPHALUS FALLAX La Rue

[Figs. 23, 56, 57, 150, 170, 178, 179]

1884: <i>Taenia ocellata</i>	Zschokke	1884:13-14, in part(?)
1884: <i>Taenia longicollis</i>	Zschokke	1884:14-15
1892: <i>Taenia filicollis</i>	Kraemer	1892:535-555
1892: <i>Taenia ocellata</i>	Kraemer	1892:572-576
1905: <i>Proteocephalus ocellata</i>	Nufer	1905 in part(?)
1905: <i>Proteocephalus longicollis</i>	Nufer	1905 in part(?)
1911: <i>Proteocephalus fallax</i>	La Rue	1911:475-477

Specific Diagnosis: Characters of the genus. Cestodes quite small. Length up to 100 mm. Maximum breadth as much as 1.20 mm. Head somewhat globose, 0.150-0.200 mm. in breadth by 0.105-0.150 mm. thick. Head well set off from neck. Suckers situated near broadest zone of head. Diameter of suckers 0.064-0.085 mm. Diameter of sucker opening about 0.040 mm. Fifth sucker present, functional, about 0.058 mm. in diameter. Neck narrow, length 2-6 mm. First proglottids quadrate or longer than broad. Mature proglottids quadrate or broader than long, 0.34-0.46 mm. broad by 0.34 mm. long. Ripe proglottids longer than broad, rarely measuring as much as 1.19 mm. broad by 1.36 mm. long. Segmentation indistinct, margins smooth.

Genital sinus marginal, alternating, situated near middle of the proglottid. Testes 30-35 in number, irregularly scattered in single layer between vitellaria and anterior to ovary. Diameter of testes 0.037-0.060 mm. Cirrus-pouch in mature proglottids 0.196-0.255 mm. long, in ripe proglottids 0.37-0.42 mm. long. Ratio of length of cirrus-pouch to breadth of proglottid 1:3-1:2. Cirrus and ductus ejaculatorius nearly straight. Length of protruded cirrus 0.026 mm. Vas deferens forming a mass of coils in middle of proglottid.

Female organs typical of genus. Vaginal opening anterior to cirrus-pouch. Vaginal sphincter weak. Ovary bilobed, lobes solid, thick, elongated ovoidal in form. In ripe proglottid ovary lies in triangular area between pouches of uterus. Vitellaria lateral, sparse. Uterus ventral,

in ripe proglottids with 6-8 lateral pouches on either side. Uterine pores 2-3 in number. Outer membrane of uterine eggs thin and hyaline, middle membrane granular, 0.036-0.041 mm., embryo 0.031-0.0336 mm. in diameter.

Habitat: Intestine of *Coregonus fera* (type host); Lake Lucerne, Switzerland (type locality).

Type: No. 09.9 in Professor H .B. Ward's collection. Slides from same lot in Professor Ward's collection.

Zschokke (1884) reported and described in a very general way five species of *Proteocephalus*. His *Taenia salmonis umblae* and *Taenia torulosa* are discussed in their proper places. The other three species, his *Taenia ocellata*, *T. filicollis*, and *T. longicollis* can best be discussed together and in this connection. The small table shows the distribution of the five species in the hosts from Lake Geneva examined by him.

Hosts	Proteocephalus Species				
<i>Coregonus fera</i>	<i>Taenia longicollis</i>	<i>Taenia ocellata</i>			<i>Taenia torulosa</i>
<i>Salmo umbla</i>	<i>T. longicollis</i>	<i>T. ocellata</i>	<i>Taenia salmonis umblae</i>		
<i>Trutta variabilis</i>	<i>T. longicollis</i>	<i>T. ocellata</i>			
<i>Perca fluviatilis</i>		<i>T. ocellata</i>		<i>Taenia filicollis</i>	
<i>Esox lucius</i>		<i>T. ocellata</i>			
<i>Lota vulgaris</i>		<i>T. ocellata</i>			<i>T. torulosa</i>
<i>Alburnus lucidus</i>					<i>T. torulosa</i>

The *Taenia filicollis* of Zschokke's description (1884:16-17) is from *Perca fluviatilis* and may be the same as the specimens from the same host species received by Dr. H. B. Ward from Professor Parona which La Rue (1911) has named *P. dubius*. It is certain that Zschokke's description and drawings of his specimens from this host do not agree with Schneider's specimens of *P. percae* (Müller).

The specimens of *T. ocellata* which Zschokke reported from *Perca fluviatilis* are probably only longer specimens of his *T. filicollis*. The specimens reported by him from *Esox lucius* were probably *Proteocephalus esocis* Schneider. It is doubtful if *Lota vulgaris* harbors the same species of parasite as does the Salmonoid fishes. Zschokke's report on

this point needs confirmation. The *Taenia longicollis* and *T. ocellata* from *Coregonus fera* are probably identical. Zschokke's description of his *Taenia longicollis* was no doubt based on specimens from *Coregonus fera* for he wrote (p. 14): "Pendant mes recherches je l'ai trouvé en grande quantité dans les appendices pyloriques et dans les intestines grêles de *Coregonus fera*, et une fois, en Février, enkysté sous sa forme larvaire dans le foie de *Salmo Umbla*."

Fortunately Dr. H. B. Ward has received some specimens from Professor Zschokke labelled, "*Taenia ocellata, Coregonus fera*." These have been found to be identical with Kraemer's *Taenia ocellata* from *Coregonus fera*, Lake Lucerne, and they have proved to be a new species to which the writer (La Rue 1911) gave the name of *P. fallax* La Rue. It is highly probable that the specimens from *Coregonus fera* identified by Zschokke (1884) as *T. longicollis* belong to this same species. The *T. longicollis* of his description differs from that of Kraemer (1892) chiefly in length. The small head, large cirrus-pouch, the proportions of the proglottids, position of the genital pore, and the size of the cirrus-pouch agree pretty well with the facts for *P. fallax* La Rue. Zschokke (1884) presented no data to show that he had made a comparative study of the specimens collected by him from *Salmo umbla* and from *Trutta variabilis*. It is scarcely possible to determine where these specimens belong, and speculation without some basis of fact is worth but little.

Kraemer (1892) as a result of his study of specimens taken from *Coregonus fera*, Lake Lucerne, in July, identified these specimens as *Taenia filicollis* Rud. Later in the same season (about Sept. 1) he took more specimens from *Coregonus fera*. These he identified as *Taenia ocellata* on account of their greater length. His specimens collected in July measured 30-60 mm. Those taken by him in September measured as much as 100 mm. Kraemer now made a careful comparison of these two forms. He found that they agreed in every particular as to size of the head and suckers and as to the presence of a fifth sucker. In the internal anatomy of the proglottids and in the histological structure of the organs the two forms also agreed perfectly. Moreover among his specimens he found gradations in length from the shortest to the longest. On these grounds Kraemer concluded that *Taenia filicollis* Rud. and *Taenia ocellata* Rud. were one and the same; that in fact the smaller *Taenia filicollis* was but an incompletely developed *Taenia ocellata*. Kraemer was correct in concluding that these larger and smaller specimens in his possession belonged to the same species. However, his conclusion has nothing whatsoever to do with Rudolphi's *Taenia ocellata* and *T. filicollis* for the very good reason that Kraemer's specimens belonged to neither of Rudolphi's species.



Kraemer in his paper gave no adequate reasons for considering that the *Taenia filicollis* and *Taenia ocellata* of Rudolphi were identical. His specimens were neither from Rudolphi's type host nor from his type locality but from a very different host and locality. Zschokke had material from *Perca fluviatilis* yet he described what he considered to be *Taenia filicollis* rather than *Taenia ocellata* from that host. Neither Zschokke nor Kraemer reported parasites from *Gasterosteus aculeatus* or *G. pungitius*, neither of which occur in the waters from which their fish came. Kraemer's specimens beyond a doubt belong to the species *P. fallax* La Rue. Riggensbach (1896) accepted Kraemer's conclusion concerning the identity of *Taenia ocellata* and *Taenia filicollis*. He apparently made no comparative study of the forms. From North American fish Benedict (1900) described a species which he considered identical with Kraemer's *Taenia ocellata* and so named it *Proteocephalus ocellata* (Rud.). That however was a misdetermination, for Benedict's specimens have been shown to belong to another species (see *P. exiguus* La Rue). Nufer (1905) may have been dealing in part with this species in his statements regarding *P. ocellatus* and *P. longicollis* from *Coregonus fera*. La Rue (1911:476-477) described this as a new species, *P. fallax*.

The material on which this species is based bears the label "*T. ocellata*, *Coregonus fera*." It was secured from Prof. Fritz Zschokke by Prof. H. B. Ward. It now bears the number 09.9 in Professor Ward's collection. Some of this material was stained in haematoxylin and mounted in balsam. Other specimens were cleared in glycerine.

A comparison of these preparations with Kraemer's description made evident the fact that this species and Kraemer's *Taenia ocellata* are anatomically identical. The fact that Kraemer's specimens were also from *Coregonus fera* and that doubtless they came from the same locality was one of the considerations which caused this identity to be suspected. Kraemer's descriptions of *T. ocellata* will be used as sources of comparative data, all of his data being grouped together.

The larger worms at the writer's disposal were unfortunately broken into pieces. One complete strobila measured 27 mm. long with a maximum breadth of 0.459 mm. A small piece in the same lot had a maximum breadth of 1.20 mm. Kraemer reported specimens of *T. ocellata* 30-60-100 mm. long. He reported a breadth of 0.114 mm. for the head and 0.038 mm. for suckers. The last measurement must be that of the sucker opening and not the maximum diameter of the sucker.

Measurements in mm. of seven scolices and suckers may be seen in the following table:

No.	Breadth of head	Length of head	Suckers, maximum diameter	Fifth sucker
1	0.187 mm.	short	0.085 mm.	not observed
2	0.185 mm.	"	0.080 mm.	" "
3	0.170 mm.	"	$0.064 \times 0.064$ mm.	" "
4*	0.185 mm.	"	0.068 mm.	" "
5	0.204 mm.	"	$0.082 \times 0.074$ mm.	" "
6	$0.153 \times 105$ mm. thick	"		" "
7	$0.187 \times 0.153$ mm. thick	"	0.079 mm.	0.058 mm.

There is here some discrepancy between Kraemer's figures and those of the writer. This may be due to an error in manipulation, to the fact that Kraemer happened to measure a very slender head, or that he happened to measure it in the dorsoventral (the shorter) dimension. As will be noted the diameter of the sucker as given by Kraemer is about the size which the writer gives for the sucker opening. The head (Figs. 23, 150) is somewhat globular in shape. The suckers are situated at or just above the broadest zone and they are directed somewhat anteriorly. In the writer's material the head is readily distinguished from the thin neck. The neck is 0.076 mm. broad (Kraemer), or 0.136 mm. broad in the writer's measurements. Kraemer states that it is long but he points out that in stained preparations part of that which appeared to be neck was in reality made up of young proglottids. In glycerine mounts the neck sometimes appeared to the writer to be as much as 6 mm. long while in stained preparation 2.38 mm. was the maximum length.

The first proglottids (Fig. 170) are about quadrate or they may be longer than broad. Kraemer gives the following breadths for the various proglottids: First long proglottids 0.228 mm. broad, the quadrate anterior proglottids 0.532 mm., the sexually ripe mid-proglottids scarcely 2.0 mm., the ripest end-proglottids as much as 2.0 mm. The writer's measurements of similar proglottids are as follows: The first proglottids 0.136 mm. broad by 0.17-0.30 mm. long, quadrate mature proglottids 0.34-0.46 mm. broad by 0.34 mm. long, the sexually ripe proglottids, 1.19 mm. broad by 1.36 mm. long (only four proglottids of this size were observed). The segmentation of the worm is indistinct, the margins being quite smooth except for very slight indentations at the junction of the segments. The segments are closely joined together. The genital

\*The opening of the suckers in No. 4 measured 0.042 mm.

pore is not marked by a papilla. The common genital sinus is marginal, irregularly alternating, and situated near or slightly anterior to the middle of the segment.

Kraemer worked out in considerable detail the structure of the cuticula, the musculature, the parenchyma, the nervous system, the excretory system, and the histological structure of the various internal organs. In the main the writer does not discuss these points, but since some of Kraemer's conclusions are incorrect the errors are indicated when possible.

In preparations studied by the writer the testes number 30-35 and they measure 0.037 by 0.053 mm. Kraemer recorded 27-30 testes with a diameter of 0.057 mm. The testes (Figs. 57, 178) lie in a single layer in the field bounded by the ovary, the anterior margin of the proglottid and the vitellaria. The cirrus-pouch is 0.196-0.255 mm. long in fully mature proglottids, where its ratio to the proglottid breadth is 1:3-1:2. In fully ripe proglottids it is more or less concealed by the uterine pouches. In a few ripe proglottids in which it was not contracted the cirrus-pouch measured 0.370-0.420 mm. in length. Apparently in this species the cirrus-pouch becomes larger after sexual maturity is attained. The cirrus-pouch is slender. Its inner end is slightly curved upward toward the dorsal surface where it is attached to the walls of the dermo-muscular sac by strong muscle fibers. This inner end (Figs. 57, 178) is usually somewhat swollen making a little vesicle. With this vesicle one or two sinuous curves of the ductus ejaculatorius may be seen. Adjacent to the vesicle is the constricted region of the cirrus-pouch. Here even in toto preparations strong circular muscle fibers may be seen. In this region the ductus passes over into the straight slender cirrus. Just beyond this constricted region the cirrus-pouch again dilates a little and here the circular muscle fibers are not prominently developed. From a cirrus-pouch so constricted the cirrus itself is usually protruded. The length of the incompletely protruded cirrus is about 0.026 mm. Kraemer states that the cirrus protrudes 2-3 mm. This must be an error, probably typographical, for a cirrus as long as 2-3 mm. would require first a very large cirrus-pouch and, second, many coils of vas deferens within the pouch. Kraemer's drawings and data are not convincing that this is the case. His figure (Fig. 178) shows a protruded cirrus probably not over 0.3 mm. in length. The vas deferens forms a mass of coils at the inner end of the cirrus-pouch. In mature proglottids this knot lies in the mid-field, even reaching past the middle.

Kraemer undoubtedly made some errors in his description of the cirrus of this species. Benedict (1900) pointed out these errors thus:



"Kraemer's description is widely different. His drawing shows a tube with hooks, representing the cirrus, and followed by a proglottis-like arrangement, and then several coils of the vas deferens within the pouch. The drawing has an unreal appearance on the first glance. The cirrus, with its curved hooks, is imbedded in the tissue, which must be torn through before it could be protruded. The proglottis-like appearance of a portion of the cirrus, as he drew it, was undoubtedly due to the way in which the circular muscles were cut in sectioning. He drew the cavity of the cirrus, into which the cut ends of the circular muscles projected, as the external outline of the cirrus. The coils would be necessary, according to his theory, but are not to be found. He says that the muscles, which he calls "the roots," are for retracting the pouch, which is sometimes thrust outwards for some distance through the opening. This protrusion is really due to an evagination of the free distal end of the inner tube."

The female organs in arrangement are typical of the genus. The vagina opens always anterior to cirrus-pouch. Near its opening at a distance of 0.041 mm. according to Kraemer, it possesses a weak sphincter muscle 0.026 mm. long by 0.034 mm. broad over all. In its course to the interovarial space it crosses the bulbous end of the cirrus-pouch or extends beyond the end of the pouch before bending posteriad. The writer has not noted in toto preparations the dilation in the middle portion of the vagina as described by Kraemer. There are no coils of the vagina anterior to the ovary. The ovary is bilobed, the lobes connected by a slender mid-piece. The lobes are solid, fairly thick bodies of elongated ovoidal shape. In mature proglottids the span of the ovary is about 0.350 mm. In ripe proglottids the ovary instead of becoming more elongated and flattened against the posterior wall of the segment shrinks in size and the two lobes become quite closely pressed together in a small triangular space (Fig. 56) bounded by the posterior proglottid margin and by the walls of the uterine pouches. This triangular space formed by uterine pouches in the posterior end of the proglottid is a very characteristic feature in this species. The vitellaria are sparse follicular glands in the lateral margins of the proglottid.

The organs of the interovarial space are probably about as Benedict has described them for his species and not entirely as Kraemer has described them. The writer has not made sections of this form and has been unable to trace the connections of the ducts. Kraemer established the presence of an oötype, an oöcapt, and a shellgland. The paired vitelline ducts do not originate as far anterior as Kraemer has figured them. They probably unite to form a single vitelline duct as in other *Proteocephalid* species where this has been investigated. Kraemer noted in toto preparations that the vagina anterior to the ovary was apparently divided, one branch going to the ovary. The second tube is probably the uterine passage which can frequently be seen in toto prepara-

tions and the connections of which can be worked out only in reconstructions of sections. The uterus is a median tube in mature proglottids. In ripe proglottids (Fig. 56, 179) there are 6-8 lateral pouches on either side of the median tube. These lie in the ventral field and come to occupy nearly the whole proglottid. By the pressure of the densely packed uterus the vitellaria are pushed farther toward the margins; the testes are pushed close to the dorsal surface and the shrunken ovaries are crowded into a small triangular space in the posterior part of the segment. The ripe proglottid is practically a thin walled sac divided up into compartments by the thin septa of the uterine pouches.

The eggs are discharged through 2-3 uterine pores (Figs. 56, 179) or through a rift down the ventral surface which is caused by a further splitting of these uterine pores. The usual number of uterine pores is 2 or 3 but occasionally a proglottid is found with a single pore. Kraemer describes a single uterine pore in the middle of the segment. The eggs have a shell with three membranes, the outer hyaline, variable in size, a middle heavier and more granular membrane, and an inner thin membrane enclosing the embryo. The embryos measure 0.031-0.0336 mm. in diameter. Such a wide variation is probably due to the different forms which the embryos assume. Some are spherical, others ovoidal. The middle membrane measures 0.036-0.041 mm. These measurements show very well the limits of variation. The outer membrane was not measured.

This species is readily differentiated from *P. percae* by its smaller head and suckers, more slender neck, and smaller proglottids. It is less robust than *P. percae*. It differs from *P. percae* in having a much shorter cirrus-pouch, fewer testes, a shorter ovary, and larger embryos. It is readily distinguished from *P. torulosus* by its smaller size and by its lack of a fifth sucker. It differs from the *P. longicollis* (Rud.) as described by von Linstow in having a smaller head with much smaller suckers. In the *P. longicollis* of von Linstow the testes are much larger than in *P. fallax* and they are in two (?) fields. The cirrus pouch is shorter in *P. longicollis*. The lateral pouches of the uterus are fewer in number and the embryos are smaller than in *P. fallax*. *P. fallax* varies from the *P. cernuae* in being more slender, with a smaller head and less muscular suckers. The latter species has broader but narrower proglottids, a shorter cirrus-pouch, more numerous and much larger testes, a longer span of ovary, and smaller embryos. *P. fallax* differs from *P. filicollis* (Rud.) in being longer, in having a fifth sucker, a longer cirrus-pouch, fewer testes, and larger embryos.

*P. fallax* much resembles *P. exiguus* but it differs from that species in having a larger head, larger suckers, a larger fifth sucker, a longer

neck, more numerous and larger proglottids, fewer testes, a shorter cirrus-pouch, and fewer uterine pouches. The embryos are larger than in *P. exiguus*. This species resembles *P. pusillus* Ward. It differs from that species in the character of the segmentation, in the smaller size of its suckers, in the position of the genital aperture, in the smaller number and size of testes, in its longer cirrus-pouch and in its fewer uterine pouches. *P. fallax* resembles *P. agonis* Barbieri but it differs from that species in being somewhat larger, in having a fifth sucker, fewer testes, and more uterine pouches. *P. fallax* is larger than *P. esocis* (Schneider) and it has a fifth sucker. It moreover has smaller and less numerous testes than *P. esocis*. *P. fallax* most closely resembles *P. dubius* but it differs from that species in having smaller and much fewer testes, a relatively shorter cirrus-pouch, fewer uterine pouches, a slightly smaller embryo, and a smaller middle egg membrane. In size, in size of head, and size of suckers they resemble each other remarkably.

#### PROTEOCEPHALUS NEGLECTUS La Rue

[Figs. 81, 82]

1911: *Proteocephalus neglectus* La Rue 1911:477

Specific Diagnosis: Characters of genus. Strobila incomplete. Head, suckers, neck not observed. Outline of proglottid rough. Segmentation evident. Genital pore on a slight prominence. Ripe proglottids 0.5 mm. long by 0.93 mm. broad to 0.75 mm. long by 1.53 mm. broad. Young and mature proglottids not observed.

Genital pores irregularly alternating, situated near middle of lateral margin of proglottid. Cirrus-pouch frequently contracted, 0.185-0.265 mm. long by 0.080 mm. broad. Normal cirrus-pouch 0.340 mm. long. Cirrus and ductus ejaculatorius straight. Vas deferens a mass of coils in mid-field of proglottid. Testes about 75, spheroidal, 0.042-0.064 mm. in diameter, situated in a single layer in space between vitellaria. Vagina anterior to cirrus-pouch, its opening dorsal to opening of cirrus-pouch. Sphincter vaginae poorly developed, situated near vaginal opening. Vagina crosses cirrus-pouch near middle. Receptaculum seminis not observed. Ovary bilobed, lobes with smooth outlines, clubshaped. Organs of interovarial space not observed. Vitellaria lateral, follicular. Vitelline follicles small, compacted. Uterus with 7-9 lateral pouches on either side. Uterine pores not seen. Embryo 0.026-0.0265 mm. in diameter. Outer egg membrane 0.042-0.047 mm.

Habitat: "Forelle" (*Trutta fario*), type host, probably from Lake Geneva or Lake Lucerne, Switzerland.



Type: Bottled material No. 09.10 in Dr. H. B. Ward's collection, and slides of same.

Some pieces of strobila without heads were received by Dr. H. B. Ward from Professor Zschokke of Basel. These were labelled "*Taenia longicollis* Rud., aus Forelle, Zschokke." The bottle is now No. 09.10 in Dr. H. B. Ward's collection. Four toto unflattened preparations were made from this material. This material formed the basis of the preliminary report, La Rue (1911:477).

Head, suckers and neck were not seen. A proglottid with eggs in the uterus measured 0.5 mm. long by 0.93 mm. broad. A ripe proglottid very full of eggs was 0.75 mm. long by 1.53 mm. broad. The outlines of the segments are rough, with several indentations on the margin of each. Proglottid limits are well defined by the indentation at the corners and by the rounded corners. A slight prominence bears the genital pore.

Genital pores alternate irregularly in the strobila. They are situated one in the middle of a lateral margin of each segment. This genital pore leads into a common atrium into which the cirrus-pouch and vagina open. When the cirrus is partly protruded the cirrus-pouch is constricted near its inner end (Fig. 81). It is also reduced in length, measuring in various states of contraction 0.185-0.190-0.220-0.265 mm. by a maximum breadth of about 0.080 mm. In a single proglottid the cirrus-pouch was in a normal condition. This is delineated (Fig. 82). This cirrus-pouch measures 0.390 mm. long. The length of the cirrus-pouch is about  $\frac{1}{4}$ - $\frac{1}{3}$  the breadth of the proglottid. Sometimes the cirrus is somewhat protruded tho it has not been seen completely protruded. It is blunt at the tip. Within the cirrus-pouch the cirrus and ductus ejaculatorius are straight. The one passes imperceptibly into the other. Coils of the vas deferens cannot be seen clearly but their confused outlines may be discerned in the middle region of the proglottid left vacant by the testes. The testes numbered 75 and 76 respectively in two proglottids in which they were counted. They are spheroidal, 0.042-0.053-0.064 mm. in diameter. It seems that they lie in one plane, filling the space between the vitellaria anterior to the ovary.

The uterus (Fig. 81) is made up of a median ventral tube from which 7-9 lateral pouches arise on either side. No uterine pores were discovered. The vitellaria are follicular and situated near the lateral margins of the segment. The follicles are small and quite compact. In the present species the vitellaria are less well developed than in *P. ceruuae*. The ovary is bilobed and is posteriorly situated. The lobes are long, thick and heavy, and have smooth outlines. In ripe proglottids the span of the ovarian lobes may be 0.60 mm. The vagina (Fig. 82) tho apparently situated anterior to the cirrus-pouch has its opening into

the genital atrium directly dorsal to the cirrus-pouch. Near its opening there is a small sphincter vaginae 0.016 mm. long by 0.010 mm. thick. Normally in its course the vagina is slightly bowed posteriad across the middle or the inner end of the cirrus-pouch. The course of the vagina in toto preparations cannot be traced to the interovarial space. The organs of the interovarial space have not been studied. The embryos measured 0.026-0.0265 mm. in diameter, the outermost envelope 0.042-0.047 mm. The second membrane was not measured.

In some respects the present species resembles *P. fallax* La Rue. The triangular shape of the interovarial space of ripe proglottids is much alike in the two species. So also there is considerable resemblance in respect to the uterine outpocketings. The proglottids, however, are as a rule broader and shorter in the present species. In the number of the testes and their close proximity to each other this species is very different from *P. fallax*. The cirrus-pouch tho greatly resembling that of *P. fallax* is relatively shorter. The two species are alike in the character of the vagina and the sphincter vaginae. Ovaries are larger in the present species. The best characters for distinguishing the two species are the number and size of the testes, the relative size of the cirrus-pouch and the size of the embryos. In some respects this species resembles *P. dubius* La Rue but the ripe proglottids are a little larger and somewhat thicker in the present species. The cirrus-pouch in proglottids of the same stage of development may be of nearly the same length. This species has more testes and these are smaller than in *P. dubius*. The chief difference lies in the size of the embryos. This difference amounts to 0.005-0.007 mm. The second membrane of the eggs of *P. dubius* is larger than the outer membrane of eggs of *P. neglectus*.

The present species differs from *P. percae* in the length of the cirrus-pouch, in the proportions of the proglottids, number and size of the testes, and in the size of the embryos. *P. neglectus* differs from *P. longicollis* as described by v. Linstow in the number, size and arrangement of the testes. The arrangement of the testes of *P. longicollis* in two fields sets that species apart from all the other species reported from fish, if von Linstow's observations on that point are correct. *P. neglectus* further differs from that species in the number of uterine pouches and in the position of the genital pore. *P. neglectus* does not agree well with Zschokke's (1884:14-16) description of *Taenia longicollis* Rud. from *Coregonus fera*. The form which he described is apparently identical with the *P. fallax* La Rue which occurs in the same host species.

## PROTEOCEPHALUS DUBIUS La Rue

[Figs. 20-22, 75-77, 147-149]

1884: <i>Taenia filicollis</i>	Zschokke	1884:16-17
1884: <i>Taenia ocellata</i>	Zschokke	1884:13-14 in part(?)
1911: <i>Proteocephalus dubius</i>	La Rue	1911:476

Specific Diagnosis: Characters of the genus. Small cestodes as much as 40 mm. long by 0.80-1.20 mm. broad. Segmentation indistinct. Proglottids about 100 in number. Head small, variable in shape, well set off from neck. Length of head 0.10-0.14 mm., breadth 0.127-0.212 mm. Four suckers 0.069-0.080 mm. in diameter, cavities deep, sucker outlines round or irregular. Fifth sucker 0.026-0.037 mm. in diameter. Neck slender 1.8-3.0-3.5 mm. long by 0.085-0.140 mm. broad. First proglottids broader than long, 0.20 mm. broad by 0.050 mm. long. Mature proglottids quadrate, broader than long, or longer than broad, 1.02 mm. long by 0.34 mm. broad to 0.595 mm. long by 0.680 mm. broad. Ripe proglottids quadrate, broader than long, or usually longer than broad, 1.19 mm. long by 0.680 mm. broad to 0.680 mm. long by 1.02 mm. broad. End-proglottid, triangular, small, functional.

Genital opening marginal, near middle of proglottid or anterior thereto, irregularly alternating. No genital papilla. Testes in two layers between vitellaria, anterior to ovary, 55-60 in number. Vas deferens a mass of coils in mid-field. Cirrus-pouch long, slender, 0.265-0.370-0.425 mm. in length by 0.070-0.085 mm. in breadth. Ratio of length of cirrus-pouch to proglottid breadth 5:11-1:2. Cirrus slender, straight, when protruded short and slender. Ductus ejaculatorius straight.

Vaginal opening anterior to cirrus-pouch. Sphincter vaginae weak, situated near vaginal opening. Vagina crosses cirrus-pouch near middle. Ovary bilobed. Lobes thick somewhat quadrate in nearly mature proglottids, smoothly ovoidal in fully mature and past-mature proglottids. Vitellaria lateral, sparse, follicles small. Uterus with 7-10-12-14 lateral pouches on either side. Uterine pores 1-2 on ventral surface. Eggs with three membranes, second membrane granular, thick, 0.042-0.053 mm. in diameter. Embryos about 0.032 mm. in diameter.

Habitat: Intestine of *Perca fluviatilis* (type host); Lake Geneva (type locality). Perhaps this species may occur also in the same host species of other lakes and rivers in southern or central Europe.

Zschokke (1884:16-17) described some specimens of cestode found by him in *Perca fluviatilis* from Lake Geneva. In some respects his description agrees fairly well with *P. fallax* La Rue from *Coregonus fera*. However in regard to the ovary there is considerable difference.



Moreover it scarcely seems probable that *Perca fluviatilis* and *Coregonus fera* normally harbor the same parasitic species. With this doubt in mind some material which Dr. H. B. Ward has received from Professor Parona labelled *Taenia ocellata* from *Perca fluviatilis* was carefully investigated. It was found that this material which at first glimpse appeared to be identical with *P. fallax* La Rue from *Coregonus fera* was after all sufficiently different to make it a separate species which was described by La Rue (1911:476) from material on which the present description is based. Material studied was alcoholic material in Professor Parona's collection labelled "*Taenia ocellata*, *Perca fluviatilis*," locality not known, and slides and alcoholics of the same in Prof. H. B. Ward's collections.

These cestodes are of small size, being short and slender. The longest specimen in Professor Parona's material measured about 40 mm. in length by about 0.80-1.2 mm. in maximum breadth. In such a specimen there are about 30 proglottids with eggs in the uterus, 12-18 mature proglottids, about 30 which show more or less developed sexual organs, and very few in which the anlagen of the sexual organs cannot be seen, in all about 80-90 proglottids. Segmentation is not very distinct for the proglottids are joined by nearly their entire breadth. The corners are slightly rounded. Zschokke stated that the margins of the proglottids are not rounded and their angles are somewhat rounded; that the animal never presents a crenated appearance and that it has the appearance of a ribbon. Zschokke found from 60-100 segments in the strobila. His longest specimen was about 4 cm. long and about 1 mm. broad.

The head (Figs. 147, 148) is of small variable shape, well set off from the neck. Frequently its anterior face is somewhat conical, at other times flattened. The head is flattened dorsoventrally. Its length varies from 0.100-0.140 mm. Its breadth is from 0.127 mm. in heads turned slightly sidewise to 0.212 mm. in slightly swollen heads. At its broadest part the head bears four suckers which are directed outward and upward. These suckers appear to be variously placed on the head depending on the state of contraction. A small fifth sucker 0.026-0.037 mm. in diameter is situated at the apex of the head. The four suckers vary in size from 0.069-0.080 mm. in diameter. They are usually nearly circular in outline but may be a little irregular. The cavity is deep and irregular in shape or it may be nearly round in outline. The neck is slender, 1.8 mm. to 3.0-3.5 mm. in length by 0.085-0.140 mm. in minimum breadth. The length of the neck was determined by measuring from the head to the first segmentation visible in stained preparations.

The following table shows dimensions of neck, head and suckers in millimeters:

Neck		Head		Suckers		Fifth Sucker
Length	Breadth	Length	Breadth	Diameter		
1.8	0.130	0.12-0.140	0.144	0.080	0.074	0.026
3.4	0.085	0.130	0.127 <sup>1</sup>	0.079	0.074	0.037
?	0.140	0.100	0.159	0.069	0.074	0.037
?	0.130	?	0.212	0.069	0.069	0.033
3-3.5	0.130	0.130	0.148	0.069	0.069	0.032

Zschokke's (1884) description of the head, suckers and neck reads:

"La tête est petite, distincte du cou, arrondie en-avant. Son pourtour est garni de quatre ventouses dont la position relative est fort variable (see Figs. 147-148).

"Ces organes de fixation sont très profonds et pourvus d'une puissante musculature. Quelquefois ils sont réunis sur une de faces, de manière qu'on peut les voir de face tous les quatre à la fois. Fréquemment elles font saillie au delà des pourtour de la tête. Celle-ci prend alors une forme libée ou frangée fort variable selon le degré de contraction des ventouses. La tête présente ainsi souvent des proéminences distribuées régulièrement. Les ventouses peuvent même affecter la forme de petites trompes protractiles.

"Le cou est long, filiforme, épaissi en-arrière; il n'occupe cependant jamais plus d'un cinquième ou d'un quart de la longueur totale de l'animal, tandis que chez le *Taenia longicollis* il atteint facilement un tiers."

There is pretty good agreement between his description and the writer's. In the writer's specimens the first proglottids are broader than long, 0.20 mm. broad by 0.05 mm. long. These soon elongate somewhat and then the anlagen of the genital organs begin to appear. The proglottids as they become mature elongate and also increase in width. They may be much elongated, nearly square or broader than long depending upon the state of contraction. In the same strobila the following measurements were taken from anterior to posterior some few proglottids being omitted at intervals, measurements of length being stated first in each instance: 1.02 by 0.34 mm.; 0.68 by 0.425 mm.; 0.595 by 0.425 mm.; 0.510 by 0.595 mm.; 0.595 by 0.680 mm. The last measurement is of the last proglottid without uterine eggs. Ripe proglottids may be nearly square, longer than broad or broader than long. They may measure as much as 1.19 long by 0.68 mm. broad; 0.68 by

<sup>1</sup>Head turned slightly sideways.

1.02 mm.; 0.68 by 0.85 mm. The end-proglottid is triangular in outline, the posterior end being rounded. It is 0.425 mm. broad by 0.476 mm. long. Apparently it is functional. No excretory pore could be seen at its posterior end. Of the proglottids Zschokke wrote: "Les premiers articles sont courts, deux à trois fois plus larges que longs. Les suivants deviennent carrés et les derniers sont ordinairement plus longs que larges. L'article terminal est arrondi en arrière. Les bords des proglottis ne sont pas bombés; leurs angles sont très peu émoussés. L'animal ne présente ainsi point de crénulure; il a l'aspect d'un ruban."

The genital opening which is situated near the middle or slightly anterior to the middle of the lateral margin of the proglottid alternates irregularly. There is no genital papilla. The testes (Figs. 75, 77) are nearly round or at times slightly compressed. They measure 0.063-0.079 mm. in diameter and they are situated in two partial layers which cover the entire field between the vitellaria anterior to the ovary. Their number is from 55 to 60. The vas deferens forms a small compact mass of coils in the midfield of the segment. The cirrus-pouch (Figs. 75, 76, 77) is long, quite slender, smooth in outline or at times somewhat constricted near the inner end by the contraction of circular muscle fibers. The cirrus-pouch measures 0.370-0.425 mm. long in ripe proglottids, 0.265-0.292 mm. long in a proglottid with few uterine eggs and 0.228-0.265 mm. in mature proglottids where the cirrus is being protruded. Its breadth is about 0.070-0.085 mm. It extends from  $5/11$  to  $1/2$  across the proglottid breadth or in some cases it may extend slightly past the middle. The cirrus is straight and slender. When protruded it may extend about 0.1 mm. past the margin of the segment. The protruded cirrus is slender or, if but slightly protruded, conical. The ductus ejaculatorius is straight and of the same size as the cirrus of which it really forms a part.

The vagina opens into the common genital sinus apparently anterior to the cirrus-pouch. Near its opening it possesses a small sphincter vaginae. The course of the vagina is slightly anteriad then posteriad and mesad in a long arc which crosses the cirrus-pouch near the middle of its dorsal side. Its entire course into the interovarial space has not been traced. A receptaculum seminis has not been observed. The ovary is posterior and is bilobed, but in nearly mature proglottids the mid-piece may not be visible. The lobes (Fig. 75) may appear as more or less irregular quadrate bodies in the posterior corners of the segment. In such a condition they resemble the ovaries which Zschokke delineated. His figure is reproduced (Fig. 149). In more mature and ripe proglottids the lobes of the ovary are smoother in contour (Figs.



76, 77). The ovarian lobes in ripe proglottids have a span of 0.425 mm. The lobes are heavier and thicker than in *P. fallax*. The organs of the interovarian space have not been observed. In the lateral fields of the proglottid lie the vitellaria, made up of small loose follicles. Well-filled uteri (Fig. 76) are made up of a median tube and 7-8-10-12 or even 14 irregular lateral pouches on either side. The more common number of pouches is 8 or 9. One large ventral uterine pore occurs quite regularly near the middle of the proglottid and a smaller pore can sometimes be found farther anteriad. Uterine eggs have three membranes. An outermost hyaline membrane is variable in size and was not measured. The second membrane is thicker, is granular and more nearly spherical. It has a diameter of 0.042-0.048-0.053 mm. tho its more common dimension is 0.048 mm. An innermost thin membrane immediately invests the embryo. The embryo has a diameter of about 0.032 mm. but when elongated it may measure 0.026 by 0.037 mm. or even 0.032 by 0.037 mm. The average measurement is about 0.032 mm.

Zschokke's description of the genital organs reads thus:

"Les orifices génitaux se trouvent au fond d'un bourrelet circulaire, situé au milieu ou un peu au-dessus des bords latéraux. L'alternance de la position à gauche ou à droite est irrégulière. Les cirrhes sont courts, coniques, leurs poches, étroites. Rudolphi parle de *ovaria quadrangularia*; en effet le parenchyme est rempli de vésicules, qui, dans les articles jeunes, ont une forme ronde ou ovale et deviennent, dans les proglottis plus mûrs, carrées et anguleuses. En réalité ces vésicules sont à l'état normal pyriformes; leur aspect carré est le résultat de leur pression réciproque. Du reste ce ne sont pas des ovaires, ce sont des testicules dont chacun présente un petit canal déférent. Tous ces canalicules se réunissent dans un canal excréteur commun.

"Déjà Dujardin, en citant la description de Rudolphi, met, derrière "ovaires opaques, également carrés", un point d'interrogation et Diesing n'en parle plus.

"Le vagin est court, il aboutit à une poche séminale assez spacieuse. L'utérus sous forme d'un tube large suit la ligne médiane du proglottis et se rend en décrivant quelques faibles lacets vers le bord postérieur de l'article. Là il décrit un noeud de lacets et se divise enfin en deux branches, qui, de leur côté, constituent à droite et à gauche une masse d'ovaires lobés ou contournés. Entre les ovaires, touchant le bord postérieur du proglottis, se trouve le glande vitellogène. Des amas glandulaires, peut-être la continuation directe des vitellogènes, se trouvent le long des bords latéraux."

This species is much smaller than *P. percae* (Müller). It is most closely related to *P. fallax* from *Coregonus fera*. It differs from that species in having regularly a larger number of testes (about twice as many as are found in *P. fallax*) and these are also larger. In *P. fallax* the testes are in one layer, in this species in two partial layers. The cirrus-pouch is usually longer than in *P. fallax* and it is relatively

longer in proportion to the proglottid width. The uterine pouches may be more numerous and the embryos a trifle larger than in *P. fallax*. The second egg membrane is larger in this species. In other respects the species are much alike. Staining and careful comparisons are necessary to distinguish them. *P. dubius* may be differentiated from *P. neglectus* by the smaller size of its proglottids and by the larger size of its embryos. The proportions of the cirrus-pouch are also very different. *P. dubius* is much unlike *P. percae* and *P. cernuae* in size, in size of suckers; in number and size and arrangement of testes, and in length of cirrus-pouch. This species differs from *P. esocis*, *P. agonis* and *P. filicollis* in size and in the presence of a fifth sucker. There is also considerable difference in the length of the cirrus-pouch.

### PROTEOCEPHALUS CERNUAE (Gmelin) La Rue

[Figs. 5, 6, 66-68]

1790:	<i>Taenia cernuae</i>	Gmelin	1790:3079, No. 79
1803:	<i>Halysis cernuae</i>	Zeder	1803:376
1810:	<i>Taenia ocellata</i>	Rudolphi	1810:108, in part
(?)1835:	<i>Taenia ocellata</i>	Von Siebold	1835:83
(?)1897:	<i>Taenia ocellata</i>	Von Rätz	1897:155,162
(?)1897:	<i>Taenia filicollis</i>	Von Rätz	1897:155, 162
1898:	<i>Ichthyotaenia ocellata</i>	Mühling	1898:37
1911:	<i>Proteocephalus cernuae</i>	La Rue	1911:475-476

Specific Diagnosis: Characters of genus. Strobila short, robust. Observed length as much as 40 mm. Maximum breadth 1.50 mm. Number of proglottids 50-60. Segmentation not plain. Head not well set off from neck, flattened dorsoventrally, and with a flat anterior face. Breadth of head 0.291-0.316 mm., length about 1.10 mm. Suckers not prominent, directed anteriorly, placed above broadest zone of head. Suckers almost globular, heavily muscled, small, with deep cavities. Diameter of suckers 0.064-0.090 mm. Fifth sucker present, 0.024 mm. in diameter. Neck 0.3-0.39 mm. broad, 1.7-2.0 mm. long. First proglottids much broader than long, 0.425 mm. broad by 0.085 mm. long. Mature and ripe proglottids broader than long. Length exceeds breadth only in old ripe proglottids. Dimensions of mature proglottids about 0.476 mm. long by 0.816 mm. broad, ripe proglottids 1.309-1.51 mm. broad by 0.68-0.85 mm. long. End-proglottid present and functional.

Common genital sinus situated near middle of lateral margin of segment, irregularly alternating. Cirrus-pouch 0.185-0.228 mm. long,

extending barely through vitellaria. Ratio of length of cirrus-pouch to breadth of proglottid 2:9 in mature, 1:5, 1:6, 1:7 in ripe proglottids. Ductus ejaculatorius in 1-3 coils. Vas deferens forming a narrow mass extending to middle of proglottid. Testes about 70 in number, in one layer, occupying entire field between vitellaria and anterior to ovary. Diameter of testes 0.085-0.130 mm. Vagina anterior to cirrus-pouch, never crossing the latter. Sphincter vaginae and receptaculum seminis not seen. Lobes of ovary thick, heavy, and long, length of pair 0.510-0.918 mm. Vitellaria coarsely follicular, voluminous, situated farther from margin of proglottid than in most species. Uterus in ripe proglottids with 6-8-9-12 lateral pouches on either side. Embryo with three membranes, second membrane 0.037-0.04 mm. in diameter, embryo ovoidal, 0.0212-0.0265 mm. in length.

Habitat: In intestine of *Acerina cernua* (Linn.).

Host	Locality	Collector	Authority
<i>Acerina cernua</i> (Linn.)	.....	Pallas	Gmelin 1790:3079.*
(?) " "	Prussia	Von Siebold	Von Siebold 1835:83
(?) " "	"	Lühe	Mühling 1898:37
(?) " "	Lake Balaton	Von Rátz	Von Rátz 1897:162
(?) " <i>schraetzer</i>	"	"	Von Rátz 1897:162
" <i>cernua</i>	Königsberg	Braun	La Rue (the present paper)

Gmelin (1790:3079) refers to this species in these words: "*Taenia cernuae*. 79—*T. Pallas elench. zooph. p.* 414. *Habitat* in percae cernuae intestinis, *vix propria species.*" The writer has not been able to secure the paper cited by Gmelin so he can not judge as to his description if, indeed, he gives one. Zeder (1803:376) adds nothing descriptive to Gmelin's data. He remarks, "*Ist schwerlich eine eigene Art, und gehört zu nro. 42. (Halysis percae mihi).*" Evidently the confusion of this species with *Proteocephalus percae* begins here. Rudolphi (1810:108) considers *T. cernuae* a synonym of *Taenia ocellata* Rud. (Vide *infra* for quotation).

Von Siebold (1835:83) found *Taenia ocellata* in *Acerina cernua* in 1834. This reference is from Mühling (1898:37). The writer has not seen von Siebold's paper. Mühling also states that Lühe in 1893 found

\*Gmelin gave this on the authority of Pallas 1776:414. The writer has not access to this work of Pallas.



this species in *Acerina cernua* but the writer has not been able to find any reference to this catch in any of Lühe's papers. Von Rátz (1897: 162) names *Ichthyotaenia ocellata* (Rud.) and *I. filicollis* (Rud.) as parasites of *Acerina cernua* Linn. and *I. filicollis* (Rud.) as a parasite of *A. schraetzer* Cuv. in Lake Balaton. Since he gives no description a determination of the systematic position of his specimens cannot be made. They may belong to *P. cernuae* and they probably do not belong to *P. percae* (Müller). Mühling (1898:17) stated that *Ichthyotaenia ocellata* had been found in East Prussia by Lühe. La Rue (1911: 475-476) described briefly *P. cernuae* from specimens used in the present description.

Von Siebold's and Lühe's specimens were collected in Prussia, the same general locality as those of Braun which the writer has had for study. For this reason and for the reason that they came from the same host species it is deemed probable that they belong to the same species. The specimens collected by von Rátz were taken from hosts occurring in a different drainage system and may or may not belong to *P. cernuae*. They probably do not belong to *P. percae* which comes from the same general region as does *P. cernuae* and which seems to be limited to *Perca fluviatilis* as a host. It is possible, of course, that they represent a new species. With these possibilities in mind von Rátz's specimens should be compared with parasites from *Perca fluviatilis* and *Acerina cernua* taken in Prussia or Finland.

The description of this species is based on five specimens which Prof. H. B. Ward secured from Prof. Max. Braun. The material bears the label "*Proteocephalus ocellata* Rud. int. *Acerina cernua* L. Königsberg, Pr. 8/93." These specimens bearing the number 09.26 and slides of the same are now to be found in Professor Ward's collection.

In general appearance these worms are short and robust. Four of them are very short, 10.0-19.5-22.0 mm. The fifth measured about 40 mm. Yet each strobila has proglottids with ripe eggs. A maximum breadth of 1.50 mm. was observed in the longest specimen and a breadth of 1.309 mm. in a shorter one. The head (Figs. 5, 6) is not well set off from the neck. Indeed, it is continuous with the neck which in all five specimens is broader than the head. The anterior face of the head is flattened and the suckers (Figs. 5, 6) are set at the margin of the flattened area. They are small and not prominent and are directed antieriad. No furrows or ridges mark the head. A fifth sucker is very faintly visible. The head is 0.291-0.316 mm. broad at a point a little posterior to the suckers. It is flattened dorsoventrally. Its length which cannot be determined with any accuracy is about 0.100 mm.

The suckers are heavily muscled, deeply concave, small and nearly globular in shape. Six suckers, four from one head and two from a second, gave the following measurements:

Suckers of *Proteocephalus cernuae*

Length	Breadth	Diameter of opening
0.07 mm.	0.079 mm.	0.042 mm. approximately
0.07 mm.	0.070 mm.	0.042 mm.
0.079 mm.	0.064 mm.	0.037 mm.
0.064 mm.	0.079 mm.	.....
0.090 mm.	0.085 mm.	0.037 mm.
0.090 mm.	0.090 mm.	0.037 mm.

The range of length and breadth of the suckers is about 0.064-0.090 mm. A sucker in transverse section measured 0.074 mm. in diameter. The sucker opening it will be observed is very small, 0.037-0.042 mm. The fifth sucker which seems to be a true sucker is about 0.024 mm. in diameter. Its cavity is very shallow. Because of the scarcity of material no sections were made and its true structure could not be finally determined. The neck in all five specimens is broad and thick, narrowest just posterior to the head. Here it measures about 0.3-0.39 mm. Its length varies from 1.36-1.7-2.0 mm. from the tip of the head to the first traces of segmentation.

The total number of proglottids in one of the shorter strobilas was 52, in the longest, 66. The segmentation is not plain. The edges of the chain are quite smooth except for now and then small folds which rarely occur at the junction of two proglottids. The angles between proglottids are scarcely noticeable. No longitudinal folds or furrows were seen. The first proglottids are much broader than long. In one specimen they measured 0.425 mm. broad by 0.085 mm. long. As the proglottids become older they increase both in length and breadth. In all but a very few ripe proglottids the breadth exceeds the length or the segments are nearly quadrate. Mature proglottids are broader than long, about 0.476 mm. long by 0.816 mm. broad. Ripe proglottids measure as much as 1.309 mm. broad by 0.68 mm. long or even 1.51 mm. broad by 0.85 mm. long. One ripe proglottid which had discharged some of its eggs measured 1.19 mm. long by 0.915 mm. broad. A true functional end-proglottid, pointed at the posterior end, was 1.19 mm. broad at the anterior end and 1.105 mm. long. The measurements given are representative hence it will be noted that in general the breadth of the proglottids exceeds the length. Only rarely and then only in old

ripe proglottids does the length exceed the breadth. The nervous and excretory systems, and the musculature have not been studied.

The common genital sinus (Figs. 66, 67) is situated very near the middle of the lateral margin of the segment or in ripe proglottids slightly posterior to the middle. It alternates irregularly. There is no genital papilla. In a worm of 52 proglottids the anlagen of the sexual organs appear in the 10th-12th segment as two darkly staining masses the one representing the cirrus and vagina and the other the ovaries. In the 20th segment the anlagen of the testes appear. Beginning with the 24th segment the sexual organs are mature while with segment 40 a number of eggs begin to appear in the uterus.

The cirrus-pouch (Figs. 66, 67) in mature proglottids is about 0.221 mm. long while in ripe proglottids its length measures 0.185-0.212-0.228 mm. It is an elongated ovoid in shape being broadest near the inner end. In mature proglottids it extends just a short distance through the vitellaria. In ripe proglottids it may barely reach through the vitellaria. The ratio of the length of the cirrus-pouch to the breadth of the proglottid varies from 2:9 in mature to 1:5, 1:6, 1:7 in ripe proglottids. The protruded cirrus has not been seen. Within the cirrus-pouch the distal portion of the cirrus is slender and straight. The ductus ejaculatorius is thrown into 1-3 coils. The vas deferens in scarcely mature proglottids is thrown into coils which extend in a straight narrow mass nearly to the middle of the proglottid, never past the middle. In ripe proglottids coils of the vas deferens are massed at the inner end of the cirrus-pouch and there is no large mass of coils in the middle of the segment. In *P. fallax* La Rue the coils of the vas deferens form a dense mass in the mid-field of the segment. In *P. neglectus* La Rue the large mass of coils of vas deferens lies in the middle of the proglottid. The testes (Fig. 67) about 70 in number, apparently lie in one layer. They are irregularly scattered between the vitellaria anterior to the ovary. They measure 0.085-0.130 mm. in diameter. They are thus more numerous and larger than in *P. fallax* and *P. dubius*, somewhat more numerous and larger than in *P. percae* and much larger than in *P. neglectus*.

The vagina (Figs. 66, 67) always opens anterior to the cirrus-pouch which it never crosses in its course to the interovarial space. It passes to the middle of the proglottid in a smooth, gentle curve, then it bends posteriad toward the interovarial space. There are no coils of vagina anterior to the ovary but at that place it may be slightly sinuous. This straight or nearly straight condition of the vagina is evidence that the worm is in a normal state of contraction for usually when a proglottid is unduly contracted the vagina is very sinuous. In



an elongated proglottid of the same worm the vagina may be straight or nearly so. Thus far a sphincter vaginae has not been demonstrated. The lumen of the vagina from its opening to the ovary is almost constant in diameter. No receptaculum seminis has been demonstrated. The ovary is bilobed as in other Proteocephalids. The lobes are thick, heavy and long. In all dimensions they are much larger than in *P. fallax* or *P. dubius*. They also have a different outline. In mature proglottids they measure 0.510 mm. long while in ripe proglottids their span may be as much as 0.918 mm. This is much greater than in *P. fallax* or *P. dubius* and more nearly like the condition in *P. percae*. The organs within the interovarial space have not been investigated.

The vitellaria (Fig. 67) are coarsely follicular, lateral masses. The follicles are much coarser and more numerous than in *P. dubius* or *P. fallax*. The vitellaria are situated at a distance of 0.100 mm. from the margin in mature and ripe proglottids. This is considerably farther than in *P. fallax* and *P. dubius* and greater than in *P. percae*. The uterus, a median tube in mature proglottids, is augmented in ripe proglottids by 6-8-9-12 lateral outpocketings on either side. The pouches (Figs. 66, 68) are long, reaching to the vitellaria, and are voluminous. Sometimes the larger pouches are apparently subdivided by short septa. For this reason the appearance of the ripe proglottid in toto preparations differs considerably from that of *P. percae* or *P. dubius*. The embryo is surrounded by three membranes, an outer thin and hyaline, a middle thick and somewhat granular, and an inner very thin membrane immediately investing the embryo. The embryo varies from ovoidal to spherical in shape. The measurements of four embryos may be taken as fairly representative of the range of size—0.0265 by 0.024 mm., 0.0212 by 0.0212 mm., 0.0265 by 0.0212 mm., 0.024 by 0.0212 mm. The second membrane measures 0.037-0.040 mm. in diameter. The outer membrane is very variable in size and in the material studied almost impossible to measure on account of its collapsed condition.

This species somewhat resembling *P. percae* and *P. torulosus* in its outward appearance is distinguished from the latter by its fifth sucker, its smaller suckers, its shorter length, its much more numerous lateral uterine pouches, its fewer testes, and by the different arrangement of testes. From *P. percae* it is distinguished by its more numerous uterine pouches, its more numerous and larger testes, its much shorter cirrus-pouch, and by the different relations of cirrus-pouch and vagina. From *P. dubius* and *P. fallax* it is distinguished by its larger head, its proglottids of greatly different proportions, its more numerous and larger testes, by the greatly different cirrus and cirrus-pouch, by the different relations of the cirrus-pouch and vagina, by the differently placed coils

of vas deferens, by the difference in the size of ovaries, and by the shape of the ovarian space in the ripe proglottid. From *P. longicollis*, as described by von Linstow, *P. cernuae* is distinguished by the much shorter neck, the different position of the genital opening, by the number of testes, by the position and shape of the mass of coils of the vas deferens, by the number of uterine pouches, and by the size of the eggs. No American species yet discovered resembles it closely.

This species is closely allied to the form which Zschokke designated as *P. longicollis* (Rud.) but which has been determined to be a separate species, *P. neglectus*. Unfortunately the heads of *P. cernuae* and *P. neglectus* cannot be compared due to lack of heads in the latter material. The shape and size of the proglottids may be about the same. In *P. neglectus* the segmentation is evident but very indistinct in this species. The minimum length of the cirrus-pouch of *P. neglectus* is greater than the maximum of the same organ in *P. cernuae*. The ductus ejaculatorius in *P. neglectus* is straight but it has from two to three coils in this species. In ripe proglottids of *P. neglectus* the ratio of the length of the cirrus-pouch to proglottid breadth is 1:3 to 2:9 but in *P. cernuae* it is 1:5, 1:6, 1:7.

The coils of the vas deferens are massed close to the cirrus pouch in *P. cernuae* but they are mostly median in *P. neglectus*. The testes of *P. cernuae* are nearly double the size of those in *P. neglectus*, so also the length of the ovary in ripe proglottids is much greater in the former than in the latter. The extent and compactness of the vitellaria and their relation to the margin of the proglottid are different in the two species. There may be more uterine outpocketings in *P. cernuae* than in *P. neglectus*. The embryo measures 0.026-0.0265 mm. in *P. neglectus* and about 0.021 mm. in spherical embryos of *P. cernuae*. A maximum measurement of 0.0265 mm. may occur in the latter species but only in elongated embryos. These species which seem much alike at first glance are thus after all quite different.

## PROTEOCEPHALUS PERCAE (Müller)

[Figs. 8, 9, 69-74, 120-122, 172, 173]

1780:	<i>Taenia percae</i>	Müller	1780:152-155, 179
1781:	<i>Taenia cystica</i>	Pallas	1781:101
1786:	<i>Taenia percae</i>	Batsch	1786:234-235
1788:	<i>Taenia percae</i>	Müller	1788:5
1788:	<i>Taenia percae</i>	Schrank	1788:48
1790:	<i>Taenia percae</i>	Gmelin	1790:3079
1802:	<i>Taenia ocellata</i>	Rudolphi	1802a:112
1803:	<i>Halysis percae</i>	Zeder	1803:355
1810:	<i>Taenia ocellata</i>	Rudolphi	1810:108.
1819:	<i>Taenia ocellata</i>	Rudolphi	1819:149
1845:	<i>Taenia ocellata</i>	Dujardin	1845:583
1850:	<i>Taenia ocellata</i>	Diesing	1850:513
1861:	<i>Taenia ocellata</i>	Van Beneden.	1861:165
1889:	<i>Taenia ocellata</i>	Lönnberg	1889:14
1902:	<i>Ichthyotaenia filicollis</i>	Schneider	1902:21-22
1902:	<i>Ichthyotaenia ocellata</i>	Schneider	1902:23
1903:	<i>Ichthyotaenia percae</i>	Schneider	1903:13-22
1905:	<i>Ichthyotaenia ocellata</i>	Schneider	1905:11-15
1905:	<i>Ichthyotaenia percae</i>	Schneider	1905:15-17
1911:	<i>Proteocephalus percae</i>	La Rue	1911:475

Specific Diagnosis: Characters of the genus. Worms of varying length, 20-200 mm. Maximum breadth 1.1-1.5-2.0 mm. Head short, broad, flattened dorsoventrally, apex slightly elevated or flattened. At summit a fifth sucker, muscular, 0.033-0.040-0.060 mm. in diameter. Four suckers, muscular, with deep cavities, 0.085-0.100-0.137 mm. in diameter, situated at broadest zone of head or immediately anterior thereto. Head 0.192-0.357 mm. broad, usually about 0.300 mm. Thickness of head 0.170-0.238 mm. Surface of head without furrows. Neck 0.170-0.50 mm. broad by 3.0-10.0 mm. long. Transition to first proglottids imperceptible. First proglottids usually broader than long, 0.255-0.34 mm. broad by 0.085-0.102 mm. long, rarely longer than broad. Mature and ripe proglottids broader than long. Breadth of mature proglottids 0.935-1.19-1.30 mm., length of same 0.255-0.340 mm. Breadth of ripe proglottids 1.10-1.7 mm.; length of same 0.42-0.85 mm. End proglottids about quadrate. Proglottids few, 150 or more, closely attached. Segmentation fairly evident, angles of proglottid rounded. Surface of worm wrinkled and rough.

Genital organs as in genus. Genital aperture marginal, near middle of proglottid, irregularly alternating. Testes in single layer, irreg-



ularly arranged between vitellaria. Testes ovoidal, 0.05-0.095 mm. long by 0.05-0.07 mm. broad, 50-60 in number. Vas deferens a thick straight mass of coils reaching to middle of proglottid or beyond. Cirrus-pouch 0.34-0.47 mm. long, slender, lying at right angles to margin of proglottid. Ratio of length of cirrus-pouch to proglottid breadth 1:3-2:5. Cirrus, when protruded 0.1-0.2 mm. long, when unprotruded, straight within cirrus-pouch.

Vagina always anterior and dorsal to cirrus-pouch, crossing cirrus-pouch near middle. Vaginal sphincter small. Lumen of vagina ciliated. Ovary bilobed, posterior. Lobes long and heavy. Vitellaria lateral, follicular, denser near ovary. Uterus with 4-5-9 lateral outpocketings on either side. Uterine pore single, situated near middle of proglottid. Eggs provided with three membranes. Embryo 0.01 mm., second membrane 0.0264-0.029 mm., outer membrane 0.031-0.037 mm. in diameter.

Habitat: Intestine of *Perca fluviatilis* and other fish.

Host	Locality	Collector	Authority
<i>Perca norvegica</i>	.....	Müller	O. F. Müller (1788)
<i>Perca fluviatilis</i>	.....	Pallas	Rudolphi (1810)
(?) <i>Acerina cernua</i> <sup>1</sup>	.....	Pallas	Rudolphi (1810)
<i>Perca fluviatilis</i>	Greifswald	Rudolphi	Rudolphi (1810)
<i>Perca fluviatilis</i>	Finland	Schneider	Schneider (1903 and 1905)
<i>Coregonus lavaretus</i>	Finland	Schneider	La Rue (The present paper)
<i>Cottus quadricornis</i> <sup>2</sup>	Finland	Schneider	La Rue (The present paper)
<i>Perca fluviatilis</i>	Rositten, East Prussia	Mühling	Mühling (1898)
(?) <i>Gasterosteus aculeatus</i> <sup>3</sup>	Rositten, East Prussia	Mühling	Mühling (1898)
<i>Perca fluviatilis</i>	Upsala	Lönnberg	Lönnberg (1889)

<sup>1</sup>In the course of this work specimens from *Acerina cernua* have been determined to belong to a new species, *Proteocephalus cernuae*. Outwardly these specimens much resemble *P. percae* and there is therefore some doubt whether the specimens collected by Pallas and the *Taenia percae* Müller were identical. Such a doubt is valid until modern investigations show that *Acerina cernua* harbors *P. percae* (Müller).

<sup>2</sup>Needs confirmation.

<sup>3</sup>This seems to be a misdetermination. The parasite was probably *P. filicollis*.

This species was first described by Müller (1780:152-155, 179). His diagnosis (1780:179) reads thus: "*Taenia percae*, capite bulboso, ocellis quatuor, ocellis marginalibus, articulis quadrangulis." On account of its inaccessibility it is deemed best to quote here a portion of Müller's observations (1780:152-153) tho in a measure these observations are recapitulated in his (1788) description which is quoted after this of 1780.

"Der Kopf oder das erste Glied des vordern und schmalen Endes ist von gleicher Breite mit den nächsten Gelenken, vorne stumpf, und in der Mitte des Randes gleichsam eingebogen. Oben mit zwei durchsichtigen und über einander stehenden kugelrunden Knoten besetzt. Wenn der Kopf fast ausgetrocknet ist, zeigt sich die Spur von vier Zirkeln, zwei an der Stelle der Knoten mit einem eingedruckten dunkeln Punkte in der Mitte; und zwei gleichsam im Schatten an der untern Lefze näher am Rande.

"Die Gelenke sind platter, und kommen einem gleichseitigen Quadrat Näher, als bei den andern Bandwürmern. Auf beiden Seiten gegen den Rand laufen *zwei helle weisse Linien* den ganzen Wurm hindurch; eigentlich werden sie, wenn man genau zusiehet, von den Verbindungen der Gelenke unterbrochen, und machen in jedem Gelenke eine kleine *bogenformige* Linie; hie und da siehet man neben den Verbindungen der Gelenke in der Mitte den gewöhnlichen punktförmigen Eindruck, und auf der einen Fläche, nicht auf der andern, einen *weissen Querstrich*, der sich von der Mitte des einen Seitenrands bis zu der Mitte des Gelenkes erstreckt. Die Gelenke sind am Rande dicker, als gewöhnlich; viele haben an dem einen äussern Seitenrande ein tiefes Loch, und, es scheint dass der Querstrich von dem hier durchfallenden Lichte herrühret, weil er an dem undurchlöchernten Gelenke, und an der Seite, wo kein Loch ist, nicht zu bemerken war. Diese Löcher sind wahre Vertiefungen, und immer in der Mitte des Seitenrandes der Gelenke, doch nicht in allen, sondern ohne Ordnung, bald in zwei, bald in mehreren auf einander folgenden. Bei den andern Bandwürmern habe ich dergleichen nicht bemerkt."

Under the name *Taenia cystica* Pallas (1781:101) described some plerocercoids which he had found encysted in the liver of the perch and pike. It seems probable that the specimens from the liver of the perch were the larval form of the *Taenia percae*. It is improbable that the larvae found in the liver of the pike belonged to this species. Rudolphi (1802a:112) states that these were probably *Tricuspidaria*. Batsch (1786:156-7) wrote concerning "Der Leberbandwurm in Barschen". Under this title he considered the larvae encysted in the livers of the pike and two species of perch which he called 'Stock-und Kaulbarschen'. His statement "die Haken und Köpfe" etc. shows very conclusively that he was dealing with some other species than *Taenia percae* tho some of his specimens may have belonged to that species. Batsch (1786:

234-5) compiled a description of *Taenia percae* from Müller's (1780) description.

Müller (1788:5) gave a description and diagnosis together with drawings of this species. The latter have been faithfully redrawn and are reproduced (Figs. 121, 122, 172, 173). These are of value for comparative purposes while the description which is here quoted is sufficiently detailed to permit its comparison with later descriptions. His diagnosis and synonymy are omitted.

"*Caput*, seu extremitas antica et tenuior insequentium articularum latitudine, obtusum supra bulbis binis sphaericis, ocularibus, pellucetibus, subtus binis similibus obsoletis infra marginem instructum. *Articuli* corporis crassiores et planiores quam in congeneribus figuram quadrangulam imitantur. In ipso corpore linea longitudinalis candida utrinque conspicitur; haec propius inspecta e lineolis articularum arcuatis quavis intersectione interruptis componitur. In ipsis intersectionibus *porus* seu osculum solitum passim conspicitur, ac marginis medio in altera paginae parts, non in opposita, linea transversa alba ad medium paginae pertingens pellucet. Haec foramini in ipsissima ora laterali quorundam articularum conspicuo ac ad medium usque pertuso deberi videtur. Foramen hoc canaliculatum oviductus est ac in paucis *Taeniae* speciebus observatur.

"In paene exsiccatō capitulo quatuor circuli bulborum vestigia apparuere; posteriores puncto opaco impressi erant.

"In intestinis *Percae marinae* raro; ultra viginti enim diversa aetate examini subiei, in duabus tantum Martio et Aprili, unicam nempe in altera, in altera tres reperi.

"Quas claris. GOEZE in *Siluro* reperit, sola absentia lineolarum lateralium non in omnibus aequè visibilibus differre videtur."

Müller in his synonymy gave *Taenia alternatim transverse lineata* Goeze, a parasite of *Silurus glanis*, as a synonym of *Taenia percae*. This was followed by Gmelin (1790:3079) who also considered Goeze's species to be the same as *Taenia percae*. Schrank (1788:48) in his catalogue gave a diagnosis of *Taenia percae* and listed the perch as the host. Rudolphi (1802a:112-13) diagnosed and described this species, naming it *Taenia ocellata*. He recognized that his species and Müller's *Taenia percae*, exclusive of the variety  $\beta$ , were synonymous. His description is here quoted verbatim:

"*Taenia ocellata*: capite obtuso, oculis orbicularibus excavatis; corpore planiusculo, articulis subquadrangulis.

"*Taenia percae* Syst. Nat. p. 3079. n. 77. (exclusa var. 3.)

"Zwei bis fünf Zoll lang. Der Kopf rundlich, der Gestalt nach alle Augenblicke verschieden, bald aufgeblasen, bald zusammengezogen u. s. w. Nach vorne stehen am Kopf vier kleine aber tiefe Saugblasen, wie Nöpfchen, an denen ich keinen Rand, wie bei der vorigen Art, wahrgenommen habe; sonst sind sie eben so veränderlich. Der Hals ist dünn und schwach runzlich, die auf ihn folgenden Glieder werden allmählich grösser und grösser, so dass die Stärksten derselben fast



eine Linie breit sind. In der Mitte eines jeden grössern Gliedes erscheinen Linien die sich untereinander verbinden und so fast das ganze Glied zuletzt einnehmen, doch habe ich keine Mündungen an den Rändern wahrnehmen können. Die Glieder sind deutlich und beinahe viereckig, man kann also nicht leicht diesen Wurm mit der *Tricuspidaria* verwechseln, wenn man auch vom Kopfe absehen wollte, das sonst schon allein statt alles Unterschiedes ist.

“Ich habe diesen Wurm, aber nur selten, im Darmkanal des Barsches, *Perca fluviatilis*, gefunden, und zwar im Junius. Pallas, der diesen Wurm unstreitig gekannt hat, (N. Nord. Beitr. I. S. 102. (113) Fig. 33. A.) verwechselt ihn mit der *Tricuspidaria*, da er ihn nicht allein im Darmkanal sondern auch in Blasen an der Leber beim Barsch (und Hecht) gefunden haben will; in diesen Blasen nämlich ist er wohl nicht zu finden.

“Müllers *Taenia percae* (Zool. Dan. II. p. 5. Tab. 44. Fig. 1-4.) scheint hierher zu gehören, der Kopf (bis auf dessen Spitze, dergleichen ich nicht finde), passt gut; was er vom Körper sagt, bezeichnet sehr grosse Exemplare, dergleichen auch Fig. 1. abbildet, ich kann also aus den Oeffnungen u. s. w. keinen Grund degegen hernehmen. Eins aber verstehe ich nicht, er sagt nämlich: *Articuli corporis crassiores et planiores quam in congeneribus*; ich finde sie auch etwas dick und abgeplättet, aber wenn sie dick sind, können sie natürlich nicht so flach seyn, als bey den ganz dünnen Arten. Uebrigens ist der Bandwurm, den Müller beschreibt, aus der *Perca marina*.

“Wenn aber Müller und auf seine Auctorität auch Gmelin den Bandwurm aus dem Wels dahin ziehen will, so kann ich nicht ihrer Meinung seyn. Sie kennen jenen Wurm nur aus Goezes Abbildung, und die ist, besonders wenn man den Kopf betrachtet, durchaus verschieden.”

Zeder (1803:355) gave a diagnosis and synonymy of this species under the name *Halysis percae*. He remarked: “Hier sind in Gmelins Ausgabe verschiedene Arten zusammengeworfen. Nach dem Zitat des Pallas (N. Nord. Beitr. S. 102) hat Gmelin den Blasenwurm aus der Leber des Barsches hieher, und zwar ganz irrig, gerechnet. Und dass der aus dem Darmkanal des Welses nicht hieher gehöret, erhellet schon aus den Bestimmungen desselben.” Rudolphi (1810:108) again diagnosed and described *Taenia ocellata*. His synonymy is almost identical with the one which has been given up to this point in this work with the exception that he considered *Taenia cernuae* to be a synonym of *Taenia ocellata*. His habitat data are here quoted: “In intestinis *Percae fluviatilis* et *cernuae* Pallas copiose, *Percae marinae* Müller rarius, repererunt. Ipse vario anni tempore in *Perca* fluv. copiosam offendi.” He considered that the variety  $\beta$  in Gmelin's (1790:3079) catalogue (*Taenia alternatim transverse lineata* Goeze) belonged with *Taenia osculata* and not here. Rudolphi (1819:149) quoted his earlier diagnosis (1810). He further stated that *Taenia ocellata* had been found abundantly by himself in *Perca fluviatilis* at Greifswald, by Pallas in *Perca cernua*, and by Müller rarely in *Perca norvegica*, a fish which Müller called *Perca marina*.

*Perca cernua* is now known as *Acerina cernua* while the *Perca marina* should be known as *Sebastes marina*, according to Jordan and Evermann (1896-1900). Rudolphi (1819) stated that *Perca marina* did not occur in Müller's region and that the latter's specimens came from *Perca norvegica*. It seems very doubtful that the species designated by Müller as *Perca marina* and by Rudolphi as *Perca norvegica* can be identical with *Sebastes marina*, for the latter is a marine fish whereas the host of *Taenia percae* must be a freshwater fish since the genus *Proteocephalus* occurs only in the fishes of freshwater. Dujardin (1845:583) and Diesing (1850:513) added almost nothing to the data as given by the earlier investigators.

Van Beneden (1861:165) briefly reported *Taenia ocellata* but gave no drawings. He stated that the perch was the host. Von Linstow (1878:208, 209) did not increase the list of hosts. Zschokke (1884:16-17) reported and described a cestode from *Perca fluviatilis*, Lake Lucerne which he identified as *Taenia filicollis* Rud. As shown in another part of this work his specimens are probably to be considered as belonging to the species, *P. dubius*. Under the name of *Taenia ocellata* Zschokke (1884:13, 14) described a form from several hosts including *Coregonus fera*. It seems not at all unlikely that this species is the same as the one from *Coregonus fera* which Kraemer (1892) first described as *Taenia filicollis* and later in the same article as *Taenia ocellata*. Kraemer's species has been shown elsewhere in this monograph to be very different from *Taenia percae*, and it was described by La Rue (1911) as a new species, *P. fallax*. A more complete discussion of Zschokke's and Kraemer's work above cited will be found in the description and synonymy of *P. fallax*. Lönnberg (1889:14) reported *Taenia ocellata* Rud. from *Perca fluviatilis*, Upsala. His diagnosis is short, yet sufficient data are given to enable one to determine that this form is not the same as that one which he reported (1889:15) from *Gasterosteus pungitius* and identified by him as *Taenia filicollis* Rud. Lönnberg's *Taenia ocellata* was nearly 3 mm. broad by 150 mm. long. It is highly probable that this form is identical with the *Taenia percae* Müller. Linton (1897:425-426) provisionally assigned to this species some cestodes which in all probability belong to *Proteocephalus ambloplitis* (Leidy). Von Rätz (1897:453) reported finding *Ichthyotaenia ocellata* in *Esox lucius* and *Lucioperca sandra* in Lake Balaton. It seems improbable that his determination was correct. Mühlhling (1898:36) found what he determined to be *Ichthyotaenia ocellata* in *Perca fluviatilis* and *Gasterosteus aculeatus* at Rositten, East Prussia. It seems probable that he has made a misdetermination in the case of the cestodes found in *Gasterosteus aculeatus*.

Schneider (1902:21-22) reported a species of cestode parasitic in *Perca fluviatilis* which he considered to be *Ichthyotaenia filicollis*. He believed this to belong to the species found by Zschokke (1884) in the same host species. He noted the fact that Kraemer (1892) considering his *Taenia filicollis* to be a younger stage of *Taenia ocellata*, put his two forms together in the same species, *T. ocellata*. To this last Schneider did not agree but held that the specimens from *Perca fluviatilis* and *Coregonus lavaretus* were distinct species. He noted on the one hand the near relationships and the great similarities of the species of the *Ichthyotaenia* and on the other extreme variability of the cestodes. He concluded that it was not therefore wholly unlikely that the one form stands in relation to the other as a variety which has arisen from the changed environmental conditions of the new host. He further gave a short description of the worm in which he considered external characters almost exclusively. In the same article Schneider (1902:23) reported some specimens of *Ichthyotaenia ocellata* from *Coregonus lavaretus* and from *Cottus quadricornis*. It seems improbable that the latter species is a host of the cestode mentioned.

Schneider (1903:13-23) decided to avoid entirely the questions of identity surrounding the names *Taenia ocellata* and *Taenia filicollis* Rud. He proposed to use the older name *Taenia percae* to designate that form from *Perca fluviatilis* which he (1902:21-22) had previously considered to be *Taenia filicollis* Rud. His reasons for this action need not be stated here. As synonyms of *Ichthyotaenia percae* he cited *Taenia percae* Müller (1788:5, pl. XLIV), *Taenia ocellata* Rudolphi (1810:108), *Taenia filicollis* Zschokke (1884:16-18) in part, *Ichthyotaenia ocellata* Riggenbach (1896:268) in part, and *Ichthyotaenia filicollis* Schneider (1902:21) in part. It is to be noted that Schneider failed to include in his synonymy any part of Kraemer's (1892) *Taenia ocellata*. This seems the more remarkable when it is remembered that both Kraemer and Riggenbach were students under Zschokke and it is quite likely that both the pupils accepted the determination of their master on the latter's *T. filicollis*. Nevertheless parts of Zschokke's and Riggenbach's data on *T. filicollis* are held to apply to *Ichthyotaenia percae*. Nor did Schneider refer to Benedict (1900) in his synonymy. In this he was correct for in another part of this work it is shown that Benedict was working on a distinct species for which La Rue (1911) has proposed the name *Proteocephalus exiguus*. In his later description of the species Schneider (1905) gave nothing further on the synonymy of *Ichthyotaenia percae* but he added some descriptive data to that given in his papers of 1902 and 1903.

Lühe (1909) considered *Taenia ocellata* Rud. a synonym of *Ichthyotaenia percae* (O. F. Müller). In his diagnosis he followed Kraemer



(1892) and as an illustration of the proglottid of the species he apparently redrew Kraemer's figure 18. Apparently also he either ignored Schneider's work or else he considered Kraemer's *T. ocellata* and Schneider's *Ichthyotaenia percae* to be identical without having made a comparison of the material. No one who has made a careful comparison of Schneider's and Kraemer's drawings and descriptions would think of putting them in the same species. It has been shown elsewhere in this monograph that Kraemer's *T. ocellata*, or *T. filicollis* as he called his species in one part of his paper, is not the same as Schneider's *Ichthyotaenia percae*. Kraemer's specimens doubtless belong to *Proteocephalus fallax* La Rue.

A comparison of Müller's (1780 and 1788) data and drawings of *Taenia percae* with Rudolphi's (1802a and 1810) diagnoses and descriptions of *Taenia ocellata* compels the writer to believe that they were referring to the same form. It is also to be remembered that Rudolphi gave Müller's *Taenia percae* as a synonym of his own *T. ocellata*. There remains no reason why the name which Müller suggested for this species should not be used instead of the name suggested by Rudolphi many years later. The generic name is *Proteocephalus*. Attention is called to the fact that Müller's figure 1 (reproduced Fig. 173) compares very favorably with Schneider's figures and with his specimens which the writer has examined. Müller's figure 4 (reproduced Fig. 172) shows the shape of the proglottids and the location of the genital organs very well. The light area extending from the margin nearly to the middle of the segment is doubtless the cirrus-pouch which under certain circumstances could have been observed by Müller. Müller's figures 2 and 3 of the heads (reproduced Fig. 121, 122) are much like the heads of Schneider's specimens which the writer has examined. Taken all in all the identification seems to be as complete as is possible without a study of Müller's and Rudolphi's actual specimens.

Since the time of Rudolphi the specific names *Taenia filicollis* and *T. ocellata* have appeared frequently in the literature of helminthology. For the most part the names are listed in reports of parasites found, without diagnosis and without description. In such cases the identity of the forms so named can not be determined with any degree of accuracy. A consideration of the host can at times throw a little light on the subject but this datum alone is not to be trusted. It is noteworthy that in the case of *Taenia filicollis* no author prior to Zschokke claimed to find this species in any other than the sticklebacks, and, indeed, in only two species of sticklebacks. Zschokke (1884) reported this species from a number of hosts, none of them sticklebacks. In the case of *Taenia ocellata* no author prior to Zschokke reported this species in any

other species than *Perca fluviatilis*, *P. norvegica*, and *Acerina cernua*. Zschokke (1884) reported this species from several hosts, and from the same host species he reported several other species of *Taenia*. A number of years later Kraemer, a pupil of Zschokke, attempted to prove that *Taenia filicollis* was the young stage of *Taenia ocellata*, and since the appearance of Kraemer's work (1892) *Taenia filicollis* and *Taenia ocellata* have for the most part been considered to be identical. As a result of the tacit acceptance of this determination great confusion exists in the identification of many lots of specimens. It is therefore difficult or, indeed, quite impossible to tell what references among the later writers should be considered in the synonymy of *Proteocephalus percae*. An actual study of many of the specimens bearing these much debated names must be made before an exact determination is possible. A comparative study of specimens of this genus now to be found in the helminthological collections in Europe would doubtless yield many interesting results. In the preparation of this monograph five lots of material identified as *Taenia ocellata* Rud. have been studied. Four of these lots were received from European investigators, another from an American. Out of these five lots four have proved to be new species reported by La Rue (1911) while the fifth was *Proteocephalus percae*. La Rue (1911:475) gave this species a place in a list of *Proteocephalus* species.

Professor Ward secured from Professor Levander, Helsingfors, Finland, some specimens of Schneider's species, *Ichthyotaenia percae* (O. F. Müller) and *I. ocellata* (Rud.) This material included both alcoholics and slides. One bottle, now No. 10.123 in Professor Ward's collection, bears the original label: "*Ichthyotaenia percae* O. F. M. Det. G. Schneider." A second bottle of this material, now No. 10.122, in Professor Ward's collection, bears the original label: "*Ichthyotaenia ocellata* Rud. *Coregonus lavaretus*. 14, V, 02." The two slides were labelled "*Ichthyotaenia ocellata*, *Coregonus*, 24, VIII, 01." From this data it seems that these must have been prepared from the same lot which Schneider mentioned in his report (1902:23 and 53). Sections and toto preparations were made from specimens of lot No. 10.123, while sections only were prepared from lot No. 10.122. Some of the heads of each lot were cleared in glycerine.

A comparison of Schneider's descriptions of his *Ichthyotaenia percae* and his *I. ocellata* show but two significant differences between the species. He states that the head of *I. percae* is much the larger but that the main difference between them is in the presence in the head of *I. ocellata* of "einen fünften flachen Saugnapf von 40 $\mu$  im Durchmesser an der Spitze, der offenbar auch noch funktioniert, da er aus

einer grossen Anzahl von Radialmuskelfasern besteht''. Of this organ in *I. percae* he writes, "an der Spitze des Scolex findet sich das deutliche Scheitel-organ, welches bei konservierten Exemplaren eine kugelförmige Anhäufung in der Längsaxe des Tieres gestreckter Zellen darstellt, die ihren Charakter als Muskelzellen offenbar verloren haben. Wir sehen hier ein rudimentäres Organ, das, wie es scheint, jede Funktion eingebüsst hat." The other differences in size and proportion of heads and necks may be explained as being due to contraction states. The breadth of the head when but a very few specimens can be measured is a valuable tho not an absolutely reliable diagnostic character in a form which is so variable and so contractile. In measuring Schneider's own specimens the writer found the heads of the two forms very much alike. One head of the *I. percae* was even smaller than the dimension recorded by Schneider for *I. ocellata*, while every head of *I. ocellata* was broader than the dimensions which he secured from measurements of the same form. Their thickness in the writer's measurements was about equal to the breadth as he recorded it. It is evident that size of head is not a valid character for the differentiation of these two forms.

As for the fifth sucker, examination of frontal sections of heads of *I. percae* with an oil immersion lens revealed the true muscular structure of a sucker. The drawing (Fig. 73) shows the nuclei, the radial muscles, basement membrane, cut ends of circular muscle fibers, and the cuticula covering the surface of the sucker. No cavity was noted in the fifth sucker of either form. This last difference then between the two forms vanishes. An examination of the two lots of Schneider's specimens revealed a marked agreement in every diagnostic feature except in the proportions of the proglottids and this slight difference was undoubtedly due to different states of contraction. Most remarkable similarity was found in the relations of the cirrus, cirrus-pouch, vas deferens, testes, vagina, vaginal sphincter, uterus, vitellaria, eggs and position of the genital pore. An examination of the comparative table and of the drawings (Figs. 8, 73, 74, 69, 70) of preparations from Kraemer's *I. ocellata* and drawings (Figs. 9, 71, 72) of his *I. percae* will at once show the strong similarities. The differences which Schneider noted in the shape of the ovary are readily explained as being due to contraction states of the proglottid. Schneider's *I. ocellata* is clearly identical with his *I. percae*, and on account of the priority of the name suggested by Müller the latter should be retained. It should also be clearly recognized that *Taenia ocellata* is a synonym of *Taenia percae* and hence can not be used to designate any other species of cestodes in this genus. Schneider then was not justified in using the name *Taenia ocellata* for the cestode found in *Coregonus lavaretus* even had it proved to be a new species.



These cestodes vary in length from 20 to 200 mm. and their maximum breadth varies from 1.1 to 1.5 to 2.0 mm. Differences in the stage of development and also in the amount of contraction account for the greater part of this variation. The short broad head (Figs. 8, 9, 121, 122) is flattened dorsoventrally. Its apex may be slightly elevated or it may be somewhat flattened. At the summit is a small but muscular fifth sucker. The four suckers, directed forward and outward, are situated at the broadest zone of the head or just anterior thereto. The breadth of the head varies from 0.192 to 0.357 mm. tho the greater number of heads measured 0.30-0.34 mm. In thickness the head measures 0.170-0.238 mm. Such variations in dimensions are due to the states of contraction of the muscles of the neck and head. Strong contractions of the longitudinal muscles of the neck and head cause the neck to dilate markedly. This condition also causes the posterior parts of the head to widen and thicken, and thus the suckers are directed more nearly forward. The converse of these statements also holds. The relaxed condition of the longitudinal muscles and the contracted condition of the neck muscles result in the narrow head. The surface of the head is smooth, without wrinkles or furrows. The four muscular suckers measure 0.085-0.100-0.137 mm., the fifth sucker 0.033-0.06 mm. in diameter. The surface of the neck is smooth tho at times transverse wrinkles simulate proglottids. The neck, usually thin, varies considerably in length and breadth. It measures 0.170-0.050 mm. broad while its length varies from 3.0 to 10.0 mm. Its transition to the first proglottids is scarcely perceptible.

First proglottids are extremely variable in shape. In a strongly contracted worm they are much broader than long, being about 0.34 mm. broad by 0.085 mm. long. In less contracted individuals these first proglottids may measure 0.255 mm. broad by 0.102 mm. long. Schneider (1903) states that they are broader than long, nearly quadrate or longer than broad. Mature and ripe proglottids show somewhat similar variations tho in less degree. Mature proglottids in all specimens examined by me were broader than long. The breadth varied from 0.935 to 1.19 or even as much as 1.30 mm., and the length from 0.255 to 0.340 mm. Fully ripe proglottids are slightly longer in proportion to breadth. They measure 1.1 mm. broad by 0.42 mm. long and in the case of the largest proglottids 1.7 mm. broad by 0.85 mm. long. No end-proglottid was observed by me. Schneider describes such a segment as being about quadrate. The number of segments varies from the few in the very short worms to 150 or more in the longer specimens (Schneider). Segmentation is fairly evident especially when the worm is viewed with a lens of low magnification, for the angles of the proglottids are rounded and the

intersegmental furrows are plainly marked. Shallow grooves and depressions give the surface of the worm a somewhat roughened appearance. The segments are firmly attached to each other.

A common genital aperture (Figs. 69, 70, 71, 72, 172) is situated near, or slightly anterior to, the middle of the margin of each proglottid. Its position in the strobila alternates irregularly from side to side. There is no genital papilla.

The testes (Figs. 69, 72) lie in a single layer between the vitellaria and anterior to the ovary. They are of ovoidal or spheroidal shape. In length and breadth they measure 0.053-0.080-0.095 mm. by 0.05-0.07 mm. In Schneider's drawing of his *I. ocellata* 50-60 testes may be seen, and in preparations from either lot of his material about that number of testes may be counted. He stated that the testes measure 0.10 by 0.06 mm. The vas deferens forms a thick straight mass of coils extending from the end of the cirrus-pouch to the middle of the segment or even a little beyond. In mature and ripe proglottids the vas deferens is always well distended with spermatozoa. Extending into the segment at right angles to the margin is the long and slender cirrus-pouch. This, in a reconstruction (Fig. 74) from a transection, may be seen to curve upward to the dorsal wall of the dermo-muscular sac where it is firmly attached by strong muscle fibers. Its length varies somewhat in proglottids of different stages of development and in different stages of contraction. It measures 0.34-0.37-0.425-0.47 mm. long, the greater lengths occurring in greatly contracted, and hence very wide, proglottids. Schneider reported the ratio of its length to the proglottid breadth as 1:3 in his *I. ocellata* and 1:3-1:2 in his *I. percae*. The writer finds the ratio in each of his forms to be from 1:3 to 2:5. In no case did the cirrus-pouch reach to the middle of the proglottid tho at first sight the coils of the vas deferens frequently gave it that appearance. Schneider saw the protruded cirrus in *I. percae*, where it measured 0.1-0.2 mm. In both of his forms he found the cirrus straight in the cirrus-pouch. The same condition was observed by the writer. Schneider did not record having seen a protruded cirrus and the writer failed to find such cirri in the material examined. From the fact that the cirrus and the ductus ejaculatorius form a straight tube in the cirrus-pouch one can safely postulate that the protruded cirrus would be short.

The vagina always opens dorsal to the cirrus-pouch. This is shown by a reconstructed transection (Fig. 74) through this region. Then passing inward and bending slightly anteriad it crosses the cirrus-pouch obliquely near the middle and passes toward the ventral wall of the dermo-muscular sac. From the point of crossing the cirrus-pouch (Fig. 72)

it passes posteriad in a long curve to the interovarial space. The vagina lies just dorsal to the uterus. Very near the opening of the vagina a short sphincter vaginae 0.020-0.026 mm. thick may be seen. The inner surface of the vagina is apparently ciliated. A receptaculum seminis has not been found, tho it may exist. The ovary (Figs. 69, 70, 72) is long and heavy. It is somewhat arched in the more elongated proglottids and more elongated and slender in the longitudinally contracted proglottids. Frontal sections show the ovary to be made up of closely connected tubes or branches. The vitellaria are long lateral follicular glands which extend from the anterior end of the segment to the ovary but not beyond. The vitellaria are more dense near the ovary.

The coils of the vagina, uterine passage, oviduct, and the common vitelline duct nearly fill the interovarial space. Here also are the oöcapt and oötype. The relations and connections of these various passages are similar to those described by Benedict (1900) for this group. An ill-defined uterine passage discharges into the uterus near the middle of the segment. The uterus (Figs. 70, 71) in ripe proglottids has 4, 5, 7, 8 or even 9 lateral outpocketings on either side. These come to fill up nearly the whole ventral side of the segment. Schneider found but a single uterine pore near the middle of the proglottid. The writer has found this number to be correct for his specimens. Schneider measured the eggs as follows: embryo 0.025 mm.; second membrane 0.045-0.050 mm.; outer membrane 0.090-0.125 mm. My measurements are made from uterine eggs of alcoholic materials. The writer has already shown (La Rue 1909) that the outer membrane swells up when it comes in contact with the water. It is not certain that the middle one does this. The writer's measurements of eggs from Schneider's material are as follows: embryo alone 0.019; second membrane, 0.0264-0.029; outer membrane, 0.031-0.037 mm. Since the writer has had Schneider's own specimens for examination he is inclined to believe that Schneider measured the embryo plus its investing membrane. The eggs which the writer so measured gave his figures almost exactly for the diameter of the embryo. It is a matter of regret that there is not more strict unanimity in the method of measuring and recording the measurements of cestode eggs. The data comprised in the discussion of the preceeding pages regarding *P. oscellatus* and *P. percae* are presented in tabular form on the next page.



Table showing comparative data on *P. ocellatus* and *P. percae*

	<i>P. ocellatus</i>	Schneider's data <i>P. percae</i>	Data secured by the writer from <i>P. ocellatus</i> , 10,122* and Schneider's slides	from Schneider's material <i>P. percae</i> , 10,123*.....
Head	0.22 mm. broad.	0.35 mm. broad.	0.34-0.357 mm. broad x 0.17(?) - 0.238 mm. thick. Head flattened dorsoventrally.	0.192-0.335 mm. broad. Head flattened dorsoventrally.
Suckers	0.08 mm. in diameter. Directed forward, and to sides.	0.075 mm. in diameter.	Diameter ranges from 0.106 to 0.137 mm. in diameter, average 0.12 mm. Opening averages 0.065 mm. in diameter. Direct- ed forward and to side.	Diameter averages about 0.09 mm. Sucker opening about 0.05 mm. in diameter. Directed for- ward and to side.
Fifth sucker	0.04 mm. Functional.	0.035 mm. Not functional.	Sucker knoblike, muscular, no cavity. 0.05-0.06 mm. in di- ameter.	Sucker knoblike, muscular, no cavity seen. 0.048 mm. in diameter.
Neck	Flattened, variable in length.	.....	0.34-0.5 mm. broad x 2-4-10 mm. long.	0.17 mm. broad x about 3 mm. long.
Strobila	170 mm. long x 2 mm. broad.	20-200 mm. long x 1.5 mm. broad.	60 mm. long x 2.0 mm. broad.	30-60 mm. long x 1.10-1.53 mm. broad.
First proglottids	Variable. Length exceeds breadth, quadrate or length equals 2.5 times breadth.	Very broad and short.	Breadth exceeds length. 0.255 mm. broad x 0.120 mm. long.	Broader than long. 0.34 mm. broad x 0.085 mm. long.
Mature proglottids	.....	.....	0.935 mm. broad x 0.34 mm. long.	1.19-1.3 mm. broad x 0.255-0.34 mm. long.
Ripe proglottids	.....	.....	1.7 mm. broad x 0.85 mm. long.	1.105 mm. broad x 0.42 mm. long.
End proglottid	About quadrate.	About quadrate.	Not seen.	No proglottids were very ripe. Not seen.
No. of proglottids	150 or more.	Variable.	.....	.....
Character of seg- mentation	.....	.....	.....	.....

\*Number of specimen in Helminthological Collection of Henry B. Ward.

Table showing comparative data on *P. ocellatus* and *P. percae* — (Continued)

	<i>P. ocellatus</i>	Schneider's data	<i>P. percae</i>	Data secured by the writer <i>P. ocellatus</i> , 10,122* and Schneider's slides	from Schneider's material <i>P. percae</i> , 10,123*
Genital aperture	Near middle of proglottid. Alternates irregularly.	Near middle or just anterior to middle of proglottid. Alternates irregularly.	Anterior to cirrus-pouch.	Evident. About middle or anterior to mid-dle. No papilla.	Evident. About middle or anterior to same. No papilla.
Vagina	Anterior to cirrus-pouch.	Anterior to cirrus-pouch.	0.025 mm. thick.	Anterior to cirrus-pouch.	Anterior to cirrus-pouch.
Vaginal sphincter	0.025 mm. thick.	0.025 mm. thick.	2 small narrow lobes.	0.026 mm. thick, short.	0.021 mm. thick, short.
Ovary	In three cornered space.	2 small narrow lobes.	2 small narrow lobes.	Lobes long, heavy. Longer and more slender in ripe proglottids.	A trifle more slender than in preceding.
Uterus	About 8 pouches on either side.	About 8 on a side or variable. Drawings show from 4 to 9.	About 8 on a side or variable. Drawings show from 4 to 9.	6-8-9 pouches on each side.	6-8-9, rarely 4-5 pouches on a side.
<div> <div>Embryo</div> <div>Middle membrane</div> <div>Outer membrane</div> </div>	.....	0.025 mm. in diameter. (Includes inner membrane.)	Eggs were taken from uterus of 0.019 mm. (embryo only).	preserved specimens. 0.019 mm. (embryo only).	preserved specimens. 0.019 mm. (embryo only).
	.....	0.045-0.05 mm. in diameter.	0.045-0.05 mm. in diameter.	0.0264-0.029 mm.	0.0264-0.0288 mm.
	.....	0.09-0.125 mm. in diameter.	0.09-0.125 mm. in diameter.	Not well developed.	0.031-0.037 mm.
Testes	10 in a transverse row. (50-60 in drawing). 0.10 x 0.06 mm. Arranged in one layer and in one field.	.....	.....	50-60, 0.053-0.08 mm. long x 0.05-0.07 mm. broad. Arranged in one layer and in one field.	50-60, 0.07-0.095 mm. long x 0.045-0.053 mm. broad. Arranged as in preceding form.
Cirrus-pouch	Reaches $\frac{3}{4}$ across breadth of proglottid.	Reaches $\frac{3}{4}$ across breadth of proglottid.	Reaches $\frac{3}{4}$ across breadth of proglottid.	Reaches $\frac{3}{4}$ across proglottid. 0.34-0.45 mm. long, slender.	Reaches $\frac{3}{4}$ across proglottid. 0.37-0.425-0.47 mm. long, slender.
Cirrus	Straight in cirrus-pouch.	Straight in cirrus-pouch. 0.1-0.2 mm. long when protruded.	Straight in cirrus-pouch. 0.1-0.2 mm. long when protruded.	Straight in pouch.	Straight in pouch.
Vas deferens	.....	.....	.....	Long straight mass of coils extending from end of cirrus-pouch to middle of proglottid.	Same as in preceding form.

\*Number of specimen in Helminthological Collection of Henry B. Ward.

An examination of the preceeding table makes evident that the differences between Schneider's *Proteocephalus percae* and his *P. ocellatus* are so slight that one would not be justified in considering these forms as varieties. Schneider dealt with a single species which according to the rule of priority should be known as *Proteocephalus percae* (Müller).

*Proteocephalus percae* in some respects resembles *P. agonis* Barbieri, *P. exiguus* La Rue and *P. pusillus* Ward. It, however, is so much larger than these species that the possibility of an identity is entirely precluded. *P. percae* in many ways resembles *P. fallax* La Rue but it is larger than that species. The character of its proglottids is greatly different. *P. percae* has many more and larger testes, a longer cirrus-pouch, a much larger ovary, more voluminous vitellaria, a larger head, larger suckers, and larger sucker openings. *P. fallax* has a larger number of preformed uterine pores. It also has larger embryos. The area occupied by the ovaries of ripe proglottids is triangular in *P. fallax* but much elongated in *P. percae*. *P. percae* resembles *P. cernuae* in the size of the head, in the size and character of the fifth sucker, in the shape of the ovary, and somewhat in the character of the proglottids. *P. percae*, however, has larger suckers with larger sucker openings, a longer and more slender neck, a much longer cirrus-pouch, and fewer and smaller testes. The relationship of cirrus-pouch and vagina are greatly different in the two species. In *P. percae* the vagina crosses the cirrus-pouch near the middle of the latter while in *P. cernuae* the vagina does not cross the cirrus-pouch. *P. cernuae* may have more uterine pouches and its embryos are larger than in *P. percae*. Further points of difference between *P. percae* and *P. cernuae* may be readily noted in an examination of the comparative table of *Proteocephalus* species (vide infra).

*P. percae* in some respects resembles *P. longicollis* as described by von Linstow but it differs in the number of uterine pouches, number of testes, length of cirrus-pouch, and in the size of eggs and of suckers. *P. percae* most closely resembles *P. pinguis* La Rue.<sup>1</sup> The heads of the two species are of about the same size. The suckers are much alike but the fifth sucker is much better developed in *P. pinguis* than in *P. percae*. *P. pinguis* is more slender, its proglottids more nearly quadrate and thicker than in *P. percae*. *P. pinguis* has many more uterine pouches and preformed uterine pores. Its cirrus-pouch is less than half as long as that of *P. percae*. *P. percae* is readily differentiated from *P. torulosus* by reason of the total lack of a fifth sucker in the latter. In number of uterine pouches, length of cirrus-pouch and in numerous other ways these species are very dissimilar.



## PROTEOCEPHALUS LONGICOLLIS (Zeder)

[Figs. 167-169]

1780:	<i>Taenia eperlani</i>	Acharius	1780:3080
1789:	<i>Taenia salmonis Wartmanni</i>	Frölich	1789:24
1790:	<i>Taenia Froelichii</i>	Gmelin	1790:3080
1800:	<i>Alyselminthus longicollis</i>	Zeder	1800:258.
1802:	<i>Taenia longicollis</i>	Rudolphi	1802a:113
1803:	<i>Halysis longicollis</i>	Zeder	1803:333
1803:	<i>Taenia Renkina</i>	Schrank	1803:242
1810:	<i>Taenia longicollis</i>	Rudolphi	1810:107
1810:	<i>Scolex tetrastomus</i>	Rudolphi	1810:6
1819:	<i>Taenia longicollis</i>	Rudolphi	1819:149
1845:	<i>Taenia longicollis</i>	Dujardin	1845:585
1850:	<i>Taenia longicollis</i>	Diesing	1850:512-513
1891:	<i>Taenia longicollis</i>	v. Linstow	1891:565-576
1891:	<i>Tetracotylus longicollis</i>	Monticelli	1891:162
1894:	<i>Ichthyotaenia longicollis</i>	Lönnberg	1894:803
1911:	<i>Proteocephalus longicollis</i>	La Rue	1911:475

Specific Diagnosis: Characters of genus. Cestodes of small size. Observed length as much as 20-200-464 mm., breadth 1-2-2.25 mm. Scolex 0.43 mm. broad, length(?). Neck 0.3 mm. broad by 3.2 mm. long. Suckers circular, 0.12-0.14-0.18-0.19 mm. in diameter. Fifth sucker half as large as others. First proglottids 0.43 mm. long by 0.71 mm. broad. Proglottids at end of first third of strobila 0.53 mm. long by 0.99 mm. broad. Posterior proglottids 1.03 mm. long by 0.83 mm. broad. End proglottid triangular.

Genital pore marginal, irregularly alternating, situated at end of anterior one-fourth of proglottid. Testes spheroidal, 0.09 mm. in diameter, 25 in each segment, arranged in two(?) fields near vitellaria. Vas deferens forming a close mass in the median field of proglottid. Cirrus-pouch spindle-shaped, muscular, 0.110 mm. broad, extending just through vitellaria. Cirrus club-shaped when everted, reaching 0.2 mm. past margin of segment. Ovary bilobed, posterior. Lobes slender, united by a midpiece. Vitellaria lateral, follicular. Uterus with three lateral pouches on either side. Vagina anterior to cirrus-pouch, not crossing same. Sphincter vaginae? Receptaculum seminis? Unripe eggs 0.0156-0.0196 mm. in diameter.

Habitat: In intestine of host.

Host	Locality	Collector	Authority
<i>Coregonus (Salmo) lavaretus</i>	Greifswald	Rudolphi	Rudolphi, 1810:107.
<i>Coregonus (Salmo) maraenula</i> = <i>C. albula</i>	Berlin	Rudolphi	Rudolphi, 1810:107.
<i>Coregonus (Salmo) wartmanni</i>	.....	Frölich	Rudolphi, 1810:107.
<i>Coregonus (Salmo) wartmanni</i>	.....	Schrank	Rudolphi, 1819:495.
<i>Coregonus wartmanni nobilis</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
<i>Coregonus fera</i>	Lake Geneva	Zschokke	Zschokke, 1884:11, 14-16.
<i>Coregonus fera</i>	Rositten, East Prussia	Mühling	Mühling, 1898:36.
<i>Coregonus albula</i>	Nicolaiken, East Prussia	Mühling	Mühling, 1898:36.
<i>Coregonus schinzii helveticus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
<i>Coregonus exiguus albellus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
<i>Osmerus eperlanus</i>	.....	Acharius	Rudolphi, 1810:212.
<i>Osmerus eperlanus</i>	Berlin	Rudolphi	Rudolphi, 1810:107.
<i>Osmerus eperlanus</i>	.....	v. Linstow	v. Linstow, 1891:565-576.
<i>Trutta trutta</i>	.....	Frölich	Rudolphi, 1810:107.
<i>Trutta trutta</i>	.....	Zeder	Rudolphi, 1810:107.
<i>Trutta fario</i>	.....	Martin	Rudolphi, 1810:107.
<i>Salmo thymallus</i> = <i>Thymallus vulgaris</i>	(in Museum Vienna)	Rudolphi	Rudolphi, 1810:107.
<i>Salmo thymallus</i> = <i>Thymallus vulgaris</i>	.....	Bremser	Rudolphi, 1819:495.
<i>Salmo alpinus</i>	.....	Martin	Rudolphi, 1810:107.
<i>Salmo salvelinus</i>	.....	.....	v. Linstow, 1878:262.
<i>Salmo salvelinus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
<i>Salmo umbla</i>	Lake Geneva	Zschokke	Zschokke, 1884:11, 14-16.
? <i>Esox lucius</i>	Lake Balaton	von Rátz	von Rátz, 1897:159.
? <i>Esox lucius</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
? <i>Perca fluviatilis</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
? <i>Alburnus lucidus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
? <i>Squalius cephalus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.
? <i>Squalius leuciscus</i>	Lake Lucerne	Nufer	Nufer, 1905:75.

Possibly this species is the form which was originally referred to by Acharius (1780:52) who called it *Taenia eperlani*. Acharius's description and diagnosis of this form are not accessible to the writer. Despite the fact that Rudolphi (1810:212) considered that this species could not have been a synonym of *Taenia longicollis* Rud. it seems that it must be a synonym of the latter species or else some of the host records of

Rudolphi and others are open to question. Concerning this species Rudolphi (1810:212) wrote:

"In *Salmonis Eperlani* cavo abdominis Taeniam reperit (pro *Fasciola habitam*) quatuor ad quinque lineas longam, capite oblongo obtuso; osculis duobus superioribus anticis (totidem inferioribus in figura latentibus) orbicularibus exiguis; collo nullo; articulis transversis, obtusis. Cum collum nullum delineatum sistatur, pro *Taenia longicollis* (n. 20) eodem in pisce obvia vix haberi potest, huic enim longissimum conceditur."

Frölich (1789:24) named a species *Taenia salmonis Wartmanni* which is recognized by Rudolphi (1802a:113 and 1810:107) as a synonym of *Taenia longicollis* Rud. Frölich's description, if he gave one, is not accessible to the writer. The name with which he designated the species is unavailable on account of its trinomial character. Gmelin (1790:3080) gave a diagnosis of *Taenia Froelichii*. This species was considered by Rudolphi (1802a:113 and 1810:107) to be a synonym of *Taenia longicollis*. Gmelin's diagnosis reads: "TAENIA FROELICHII. No. 91.—T. capite cum collo longissimo tenuissimo marticulato continuo, ovarii dendaticis linea laterali cinctis. *Froelich Naturf.* 24 p. 124. t. 4. f. 20. 21. *Habitat in Salmonis Wartmanni intestino duodeno.*"

The name *longicollis* as a designation for a species of cestode was first used by Zeder (1800:258) in connection with the generic name *Alyselminthus*. Unfortunately Zeder's description is not available to the writer who therefore can not judge as to its character. Rudolphi (1802a:113) gave a specific diagnosis of this species which he styled *Taenia longicollis*. In his synonymy he cited *Alyselminthus longicollis* Zeder, *Taenia Salmonis Wartmanni* Froelich, and *Taenia Froelichii* Gmelin. After a statement regarding the hosts of this form he wrote:

"Zeders Beschreibung ist vollkommen genügend; wenn er Frölich tadelt, weil dieser die bäumschenartigen Figuren oder Eyerstöcke der Glieder mit zur Bestimmung des Wurms braucht, so habe ich im Allgemeinen nichts dagegen, dass man sie weglässt. Bey einigen Arten sind sie indessen besonders ausgezeichnet, so auch hier, wo man sie auf den ersten Blick gewahr wird, weswegen auch die letzten Glieder bläulich, oft sogar schwärzlich aussehen. Wo man erst den Pressschieber zu Hülfe nehmen muss, um sie zu sehen, darf man ihrer nicht erwähnen, das versteht sich."

Rudolphi gave no description of this species at this time nor were there any drawings to accompany his comments. Zeder (1803:333) referred to this species under the name *Halysis longicollis*. In his synonymy he lists *Taenia salmonis Wartmanni* Frölich, *Alyselminthus longicollis* Zeder, *Taenia Frölichii* Gmelin. His diagnosis reads: "HALY-



SIS LONGICOLLIS.—leviter crenata; capite cum collo longissimo, lineari continuo, truncato; osculorum margine prominente.”

Rudolphi (1810:107) gave a diagnosis and description which is here quoted verbatim:

“*Taenia longicollis* R.

*Taenia*: capite truncato, collo longissimo, articulis subquadratis, ovariis racemosis.

Frölich im Naturforsch. 24.p.124. Tab.4. fig.20.21. *Taenia Salmonis Wartmanni*.

Gmel. Syst. Nat. p. 3080. n. 91. *Taenia Froelichii*.

Zeder Nachtrag p. 258. *Alyselminthus longicollis*.

Rudolphi in Wied. Arch. III. 1.p.113. *Taenia longic.*

Zeder Naturg. p. 333. n. 9. *Halysis longic.*

“Hab. in intestinis Salmonum. In *Salmonibus Wartmanni* plurimis Froelichius Augusto copiosam; in *S. Trutta* Zederus; ego in *S. Lavareto* Majo et *S. Maraenulis* plurimis Februario, reperimus. In *Salmone Eperlano* a se inventas am. Treviranus mecum communicavit.

“Descr. Vermes unum ad septum pollices longi, lineam dimidiam vel integram lati.

“*Caput* depressum, truncatum, exiguum; *osculis* orbicularibus, binis tam superioribus, quam inferioribus, capitis margini antico approximatis, ut sub ejusdem motu saepe antica omniaque simul appareant. *Collum* cum capite continuum, longissimum, tertiam circiter totius longitudinis partem sibi vindicans, depressum, margine obtuso integerrimo. *Corpus* depressum, articulus anterioribus brevissimis, reliquis subquadratis, marginibus singulorum antico et postico rectis, lateralibus rotundatis, ut totius vermis latera crenata appareant. Articulus ultimus obtusus. *Ovaria* in articulis posticis, inde vel caeruleiscentibus, vel nigrescentibus, distincta, racemosa sive dendritica.

“Obs. 1. An scolex tetrastomus supra dictus hujus *Taenia* proles nondum articulata? Sed reliquarum *Taeniarum* foetus semper articulatos vidi, neque caput, neque pars postica acuta conveniunt.

“Obs. 2. Hujus speciei cum insequentibus ob articulos margine postico vix incumbentes, ob capitis collique formam, affinitas magna; differentiae tamen specificae singularum discrimen satis indicant.

“Obs. 3. An quas Stellerus (Pallas N. Nord. Beytr. I.1, p.102) in *Eperlani vesica natatoria* reperit, *Taenia* huc pertinent? Conf. n. 113.”

Rudolphi (1819:149) quoted the diagnosis used by him before (Rudolphi, 1810:107). He stated that he had found the species in *Coregonus (Salmo) lavaretus* at Greifswald, in *C. (Salmo) maraenula*=*C. albula* and in *Osmerus eperlanus* at Berlin, that Frölich had found it in *Coregonus (Salmo) wartmanni*, Frölich and Zeder in *Trutta trutta*. Specimens in the museum at Vienna had been found in *Salmo thymallus*=*Thymallus vulgaris*. He further stated that Martin had found it in *Salmo alpinus* and in *Trutta fario*. This serves as a very excellent

summary of the hosts which had been recorded for this species up to this time. Rudolphi (1819:495) stated that Bremser's specimens which had been taken in the pyloric caeca of *Salmo thymallus* belonged to *Taenia longicollis* and not to *Bothriocephalus*. He further stated that *Taenia Renkina* Schrank is identical with *Taenia longicollis* because *Salmo Wartmanni* is called *Renken* in central Germany. Schrank's (1803:242) description of *Taenia renkina* is not at hand hence it is necessary to follow Rudolphi's judgment in the matter. Dujardin (1845:585) added but little to the data of the earlier authors. Diesing (1850:512-13) gave a literature review that is of value. Von Linstow (1878:262) in his catalogue of entozoa gave *Salmo salvelinus* as a host of this species.

Zschokke (1884:11, 14-16) identified and described some cestodes from *Coregonus fera* and *Salmo umbla*, Lake Geneva, as *Taenia longicollis*. A careful comparison of his descriptions of *T. longicollis* and *T. ocellata*, likewise reported by him from the same hosts, causes the writer to conclude that his specimens belonged to the same species. Length forms the chief difference between his species. In describing certain organs of the two forms he used almost identical phrases. Kraemer (1892) in his study of *Taenia ocellata* evidently used length as the chief distinguishing character. Zschokke's description of *T. longicollis* does not agree with the description and figures of that form as given by von Linstow (1891:565-576). Von Linstow's specimens were taken from *Coregonus eperlanus*, one of the hosts in which Rudolphi found *T. longicollis*. It is therefore probable that von Linstow's specimens rather than Zschokke's belong to Rudolphi's species. Moreover, von Linstow's description agrees more completely with Rudolphi's than does Zschokke's. Lönnberg (1894:803) included *Taenia longicollis* Rud. in the list of species in his genus *Ichthyotaenia*.

Zschokke (1896:772-777) listed *Ichthyotaenia longicollis* only in *Trutta fario* from Lake Geneva. Thanks to Prof. H. B. Ward, the writer has been able to examine parts of a strobila of Zschokke's "*T. longicollis* aus Forelle" (*Trutta fario*) and is able to state positively that it is not the same species as von Linstow's *T. longicollis*. Nor is it the same as the specimens from *Coregonus fera* which Zschokke sent to Professor Ward as *T. ocellata* (No. 0.99 in Prof. H. B. Ward's collection, the type of *P. fallax* La Rue). Von Rátz (1897:159) listed *Ichthyotaenia longicollis* from *Esox lucius* from Lake Balaton in Hungary. This is probably a misdetermination. Von Rátz gave no description so not even a probable determination can be made. Mühlhing (1898:36) reported *Ichthyotaenia longicollis* Rud. from *Coregonus albula* at Nicolaiken and from *Osmerus eperlanus* at Rositten in East Prussia. He

gave no description. Nufer (1905:75) in the report of an investigation of Lake Lucerne reported *Proteocephalus longicollis* from *Perca fluviatilis*, *Alburnus lucidus*, *Squalius cephalus*, *S. leuciscus*, *Esox lucius*, *Coregonus wartmanni nobilis*, *C. exiguus albellus*, *C. schinzii helveticus* and *Salmo salvelinus*. It is extremely doubtful if the specimens of *Proteocephalus* which Nufer found in other than the salmonoid fishes belong to the species *P. longicollis*. Nufer's tabulated description of *P. longicollis* (Nufer 1905:147) is based almost entirely upon the work of von Linstow (1891). The character of Nufer's work has been discussed at some length in connection with *P. macrocephalus* and *P. torulosus*. Many of the statements made in those places regarding his work apply here.

A discussion of the facts brought out in this historical summary cannot yield very satisfactory conclusions. For the most part the authors cited have necessarily been compelled to depend upon the external features of the worm for diagnostic characters. Benedict (1900) showed how little dependence could be placed on such characters alone for descriptive purposes. The earlier workers necessarily based their conclusions on little else than external features, upon records of hosts, and locality of collection. The host records of all the workers who reported this species prior to Nufer and von Rátz show that these men regarded this species as being peculiar to the salmonoid fishes and it seems quite probable that they were correct in this respect. It is impossible to determine whether this species is parasitic in all the salmonoid fishes of the list or whether a number of cestode species have been reported under the one name without a painstaking comparative study of such specimens as exist in private and museum collections together with a study of specimens from hosts and localities as indicated in the list of hosts. It is not likely that this will be done, at least not for some time.

The question of priority of name is not an important one. This species is known as one of Rudolphi's species probably on account of the weight of Rudolphi's authority as much as on anything else. His first notes on this species contain only the briefest diagnosis and he distinctly says, "Zeders Beschreibung ist vollkommen genügend", etc, etc (vide supra). In the light of this it seems that Zeder should be credited with the specific name *longicollis*. It is true of course that Rudolphi was the first to use the combination *Taenia longicollis*. As to the use of the name *longicollis* or some of the names that were proposed still earlier, viz., *Taenia Froelichii*, *T. salmonis wartmanni* and *T. eperlani*, it may be said that the identity of the last is not well known. Rudolphi (1819) thought it was not identical with *T. longicollis*. *T. sal-*



*monis Wartmanni* being a descriptive name of three parts is not available. It is not necessary to discuss the question as to whether it was sufficiently described to give it any standing. *T. Froelichii* was evidently based on the same description as the *T. salmonis Wartmanni* for Gmelin (1790) gives little more than a catalogue of species and refers to Froelich's (1789) work. Since the combination *Taenia longicollis* Rudolphi is no longer the proper one with which to designate this species, the generic name *Proteocephalus* being used to designate the genus, it is here suggested that the proper combination for the designation of the species is *Proteocephalus longicollis* (Zeder). In a recent article the writer, La Rue (1911:475), overlooked the priority of Zeder's *Alyselminthus longicollis* over Rudolphi's *Taenia longicollis* and hence in a list of species of *Proteocephalus* gave the credit for the *P. longicollis* to Rudolphi instead of Zeder.

The description is based on von Linstow's (1891) paper. His material was collected from *Osmerus eperlanus* which is one of the hosts in which Rudolphi found *Taenia longicollis*.

Von Linstow reports that his largest specimen measured 46.4 mm. long by a maximum breadth of 0.99 mm. At its posterior end the worm measured 0.83 mm. broad. The scolex measured 0.43 mm. broad, the neck 0.3 mm. broad by 3.2 mm. long, first proglottids 0.43 mm. long by 0.71 mm. broad, proglottids at end of first third of strobila 0.53 mm. long by 0.99 mm. broad. The proglottids gradually increase in length until the last are 1.03 mm. long by 0.83 mm. broad. The end-proglottid is triangular and drawn out posteriorly. The specimen was incompletely developed. The four suckers have a circular outline, 0.12-0.14-0.18-0.19 mm. in diameter. A fifth apical sucker has a diameter equal to one-half that of the others.

The excretory system is made up of two large lateral vessels, one on either side just outside of the vitellaria, and six smaller vessels, three on either side lying dorsal to the larger vessel. All excretory vessels are greatly twisted and many anastomoses connect them. About 0.08 mm. anterior to the posterior margin of each proglottid a transverse commissure connects the ventral excretory vessels. The latter measure 0.019 in diameter and the smaller vessels about 0.0078 mm. In the region just posterior to the suckers there is a circular commissure of excretory vessels from which branches extend anteriorly into the head. All the main vessels discharge into a small vesicle at the posterior end of the end-proglottid.

The genital pore is marginal, irregularly alternating, and situated near the end of the anterior one-fourth of the proglottid (Fig. 167). The testes are large, spheroidal, measuring up to 0.09 mm. in diameter.

Von Linstow states that there are about 25 testes in each segment, and that these are situated in two fields near the vitellaria. In a drawing of a transverse section, reproduced (Fig. 168), von Linstow figures the testes in two layers. This causes the writer to suspect that the number of testes (25) as stated by von Linstow is too small. In all the species of *Proteocephalus* studied by the writer the testes have been in one layer if the number of testes was small and never in two layers unless they numbered at least fifty. Frequently one sees proglottids containing more than fifty testes lying in a single layer. It should also be borne in mind that von Linstow figured ten testes in his cross-section of the proglottid. Ten out of twenty-five is too large a proportion of testes to appear in one thin section through proglottids of this size. One wonders what was left for the other sections of which there must have been quite a number. Since the proglottid which von Linstow delineates is ripe or at least contained eggs in the uterus it seems probable that he overlooked the testes of the median region where the eggs would be densely packed. In the transverse section to which reference has been made the region dorsal to the coils of vas deferens is free from testes, a condition which exists in all the other species of the genus whether the number of the testes be few or many. If von Linstow's statement that the testes lie in two lateral fields be correct then this species is the only exception to the rule that the testes in this genus are irregularly scattered in the field between the lateral vitellaria. The considerations above presented cause one to doubt the accuracy of von Linstow's statements regarding the number and position of the testes. The vas deferens forms a thick mass of coils in the middle of the proglottid. This mass apparently does not extend over to the cirrus-pouch. In von Linstow's figure the cirrus-pouch, which he describes as a spindle-shaped muscular organ with a breadth of 0.110 mm., extends just a little within the vitellaria, or about  $\frac{1}{4}$ - $\frac{1}{5}$  across the proglottid. The cirrus (Fig. 169) in the 46.4 mm. specimen was visible at a point 13.8 mm. posterior to the head. It is short and club-shaped, 0.34 mm. long, and it extends 0.2 mm. beyond the proglottid's margin.

A comparison of cirrus-pouches in Von Linstow's figures (reproduced Figs. 167 and 169) shows some evident discrepancies. The cirrus-pouch in Figure 167 is set far within the tissues of the proglottid and it is connected with the exterior by a slender tube. Figure 169 shows by far the more typical condition and is to be considered as the normal for this species.

The bilobed ovary lies in the posterior part of the proglottid. The lobes are club-shaped. The vitellaria lie in the lateral fields. They discharge the yolk-cells through the paired vitelline ducts which pass to

the interovarial space where they unite to form a common duct that empties into the oötype. Thus far von Linstow is correct in his description of the organs of the interovarial space. According to him the vagina discharges into the oötype as do also the two lobes of the ovary. He provides no visible means for the escape of the fertilized eggs from the oötype. The writer agrees with Monticelli (1891:162) in thinking that von Linstow has probably mistaken the oöcapt for the oötype, and has erroneously figured the vitelline ducts which pass near the oöcapt and the shell-glands lying near as discharging into it. The barrel-like form of the oötype as he figures it (Fig. 167) is much more typical of the oöcapt. The oötype has its long axis lying lengthwise of the oviduct and not perpendicular to it. The vagina in von Linstow's figure is doubtless the oviduct. There is every reason to believe that the organs of the interovarial space bear the same relations to each other in this species as they do in the other members of the genus. The vagina opens into the common genital sinus always anterior to the cirrus-pouch. Without crossing the latter the vagina describes a curved course to the interovarial space where it forms several coils. Von Linstow did not mention the presence of a sphincter vaginae. The uterus has three large lateral pouches on either side. A uterine pore is lacking. The latter could perhaps be found after a careful examination. The unripe eggs measure 0.0156-0.0196 mm. in diameter. The plerocercoid of this species is found in the liver of the host in which the adult is found.

It is evident from a study of Von Linstow's figures and text that he made several misinterpretations of the structural plan of this cestode. He recognized that its plan differed in certain respects from the plan on which the Taenias are formed for he said that the Taenias of fish formed a distinct group in the genus Taenia. He apparently did not note the marked resemblance of their plan to the plan of the Tetraphyllideans. Whether his failure to recognize the relationships of this species was the cause or the effect of his misinterpretation of its structure cannot be determined. At any rate because of some doubtful points his material should be re-examined and a comparative study made if such be possible.

This species is readily separated from the *P. torulosus* by its fifth sucker, and by its somewhat smaller head and smaller suckers. The ovarian lobes are more slender in this species than in *P. torulosus*. *P. longicollis* is readily differentiated from *P. percae* by its larger head, larger suckers, shorter cirrus-pouch, fewer (?) testes, fewer uterine pouches and by the position of the genital pore. *P. longicollis* resembles *P. cernuae* in a very few particulars such as shortness of cirrus-pouch. However, *P. longicollis* has a larger head, larger suckers, fewer uterine



pouches, smaller embryos, fewer and smaller testes which are differently arranged. *P. longicollis* is much larger than *P. fallax* La Rue and *P. dubius* La Rue and it differs further in having fewer uterine pouches, a shorter cirrus-pouch, fewer (?) and larger testes. The genital pore is further anteriad in *P. longicollis* than in *P. fallax* or *P. dubius*. *P. longicollis* differs from *P. dubius* La Rue in having fewer uterine pouches, a shorter cirrus-pouch, fewer and larger testes and a different arrangement of the same. *P. longicollis* does not closely resemble any species reported from North America up to the present time.

### PROTEOCEPHALUS TORULOSUS (Batsch)

[Figs. 7, 78-80, 145, 146, 184]

1782:	<i>Taenia articulalis rotundis</i>	Bloch	1782:11
1786:	<i>Taenia torulosa</i>	Batsch	1786:181-182
1788:	<i>Taenia orbicularis</i>	Schrank	1788:49
1791:	<i>Taenia simplex</i>	Frölich	1791:58-61
1790:	<i>Taenia torulosa</i>	Gmelin	1790:3081
1795:	<i>Taenia cyprini idi</i>	Viborg	1795:240
1800:	<i>Rhytelminthus cyprini</i>	Zeder	1800:215, 220
1802:	<i>Taenia torulosa</i>	Rudolphi	1802a:110-112
1803:	<i>Halysis torulosa</i>	Zeder	1803:352-353
1810:	<i>Taenia torulosa</i>	Rudolphi	1810:111
1819:	<i>Taenia torulosa</i>	Rudolphi	1819:149-150
1845:	<i>Taenia torulosa</i>	Dujardin	1845:584
1850:	<i>Taenia torulosa</i>	Diesing	1850:514
1861:	<i>Taenia porulosa</i>	Van Beneden	1861:162-163
1884:	<i>Taenia torulosa</i>	Zschokke	1884:20, in part
1889:	<i>Taenia torulosa</i>	Lönnberg	1889:15
1891:	<i>Taenia torulosa</i>	von Linstow	1891:565
1892:	<i>Taenia torulosa</i>	Krämer	1892:55
1894:	<i>Ichthyotaenia torulosa</i>	Lönnberg	1894:801-803
1896:	<i>Ichthyotaenia torulosa</i>	Zschokke	1896:775
1897:	<i>Ichthyotaenia torulosa</i>	von Rätz	1897:159
1901:	<i>Ichthyotaenia torulosa</i>	Frič & Vavra	1901:111-112
1902:	<i>Ichthyotaenia torulosa</i>	Schneider	1902:24
1905:	<i>Ichthyotaenia torulosa</i>	Schneider	1905:24-25
1905:	<i>Proteocephalus torulosus</i>	Nufer	1905:75, 147, in part
1909:	<i>Ichthyotaenia torulosa</i>	Lühe	1909:32
1911:	<i>Proteocephalus torulosus</i>	La Rue	1911:475

**Specific Diagnosis:** Characters of the genus. Large cestodes 65-600 mm. long by 1.2-2.25 mm. broad. Head large, prominent, swollen, flattened dorsoventrally, without rostellum, without fifth sucker. Breadth of head 0.480-0.600 mm., thickness about 0.300 mm. Suckers circular, prominent, with deep cavities, directed anteriorly and outward. Diameter of sucker 0.18-0.20 mm. Neck thick, broad, 2-3 mm. long, wrinkled. First proglottids much broader than long, mature and ripe proglottids almost always broader than long. Maximum length of ripe proglottids 1.0 mm., maximum breadth of same 2.5 mm. Proglottids fleshy, well delimited by deep inter-segmental furrows, corners of segments prominent. End-proglottid rounded posteriorly. In its posterior end a deep indentation.

Genital pore irregularly alternating, situated near middle of lateral proglottid margin. Vaginal opening dorsal and anterior to opening of cirrus-pouch. Cirrus-pouch and vagina opening into a common genital sinus. Testes large, 0.16 by 0.08 mm., 100-110 in number. Testes in two layers, one occupying the whole dorsal field between vitellaria, completely covering ovary. Vas deferens, an eccentric mass of coils reaching from cirrus-pouch to middle of proglottid. Cirrus-pouch about 0.255 mm. long by 0.085 mm. broad, extending  $\frac{1}{4}$ - $\frac{1}{6}$  across proglottid breadth. Cirrus short, not heavy. Ductus ejaculatorius describing few or no coils.

Vaginal opening dorsal and anterior to cirrus-pouch. Sphincter vaginae very weak, situated near vaginal opening. Vagina not crossing cirrus-pouch. Vitellaria lateral, voluminous, follicles large and closely packed together. Ovary bilobed, lobes long, thick, and irregular in outline. Oötype and oöcapt present. Uterus in ripe proglottids with 3-4 lateral pouches on either side. Uterine pores not observed. Eggs provided with three membranes. Outer membrane hyaline, 0.055 mm., second membrane granular, 0.032 mm., embryo about 0.021 mm. in diameter.

## Habitat: In intestine of host.

Host	Locality	Collector	Authority
<i>Idus melanotus</i> ( <i>Cyprinus jesus</i> ) (type host)			Batsch (1786:181-182)
<i>Idus melanotus</i> ( <i>Cyprinus jesus</i> )	Berlin	Bloch	Rudolphi (1819:150)
<i>Idus melanotus</i> ( <i>Cyprinus jesus</i> )	Greifswald	Rudolphi	Rudolphi (1819:150)
<i>Idus melanotus</i> ( <i>Cyprinus orfus</i> )		Frölich	Rudolphi (1819:150)
<i>Leuciscus leuciscus</i>		Zeder	Rudolphi (1819:150)
<i>Leuciscus leuciscus</i>			von Linstow (1878:254)
<i>Leuciscus leuciscus</i>	Podiebrad, Bohemia	Frič and Vavra	Frič & Vavra (1901:111-112)
<i>Leuciscus leuciscus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
<i>Idus melanotus</i> ( <i>Leuciscus idus</i> )		Abildgaard	Diesing (1850:559)
<i>Idus melanotus</i> ( <i>Leuciscus idus</i> )	(In M. C. V.)		Diesing (1850:514)
<i>Idus melanotus</i> ( <i>Leuciscus idus</i> )	Finland	Schneider	Schneider (1902:24 & 1905:24-25)
<i>Leuciscus grislagine</i>	Sweden (?)	Tullberg	Lönnberg (1889:15)
<i>Alburnus bipunctatus</i>	(In M. C. V.)	Diesing	Diesing (1850:514)
<i>Alburnus sp.</i>		Creplin	Diesing (1850:514)
<i>Alburnus lucidus</i>			von Linstow (1878:258)
<i>Alburnus lucidus</i>	Lake Geneva	Zschokke	Zschokke (1884:20)
<i>Alburnus lucidus</i>	Lake Lucerne	Kraemer	Kraemer (1892:55-71)
<i>Alburnus lucidus</i>		von Linstow	von Linstow (1891:565)
<i>Alburnus lucidus</i>		Zschokke	Zschokke (1896:775)
<i>Alburnus lucidus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
<i>Aspius rapax</i>		Creplin	Diesing (1850:514)
<i>Abramis brama</i>			von Linstow (1878:258)
<i>Abramis brama</i>	Lake Balaton	von Rátz	von Rátz (1897:159)
<i>Idus melanotus</i>			von Linstow (1878:255)
<i>Pelecus cultratus</i>	Lake Balaton	von Rátz	von Rátz (1897:159)
<i>Gobio fluviatilis</i>	Lake Lucerne	Nufer	Nufer (1905:75)
<i>Squalius leuciscus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
<i>Blicca bjoerkna</i>	Lake Lucerne	Nufer	Nufer (1905:75)
(?) <i>Coregonus fera</i>	Lake Geneva	Zschokke	Zschokke (1884:20)
(?) <i>Coregonus exiguus albellus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
(?) <i>Coregonus schinzi helveticus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
(?) <i>Salmo salvelinus</i>	Lake Lucerne	Nufer	Nufer (1905:75)
(?) <i>Perca fluviatilis</i>	Lake Lucerne	Nufer	Nufer (1905:75)
(?) <i>Perca fluviatilis</i>	Podiebrad, Bohemia	Frič and Vavra	Frič & Vavra (1901:111-112)
(?) <i>Lota vulgaris</i>	Lake Geneva	Zschokke	Zschokke (1884:20)



Batsch (1786:181-182) first described this species from *Cyprinus jesus* giving it the name *Taenia torulosa*. His description is here quoted in full:

"*Taenia torulosa*. Der rundgliedrige Bandwurm.

"Bloch Preisschr. S. II nr. 4. T. 2. fig. 1-4. 10. 11. *Taenia articulis rotundis*. Der rundgliedrige Bandwurm.

*Taenia* (loriformis) capite inermi, obtuso, oculis per paria difformibus: corpore toruloso, articulis orbicularibus collo crenato, elongata.

"Diese und die folgende Art haben einen abgestumpften, die nächsten fünf aber einen stumpfspitzigen Scheitel, bei allen sind weder die Haken, noch der besondere Rüssel vorhanden wie bei denen vier vorigen.

"Der rundgliedrige Bandwurm hat rundliche Glieder, die kurz, dick, und undurchsichtig, und wie eine Korallenschnur an einandergereiht sind. Am Rande die Mündungen.

"Der Hals ist kurz.

"Der Kopf bewegt seine vier Saugmündungen paarweis, bald in halbmondförmige Wülste, bald in die Gestalt eirunder Oeffnungen. Bisweilen erweitert er sie alle vier in eine zirkelrunde Form, und alsdenn verschwindet ihr sonst sichtbarer Ring.

"Die Eier gehen unter dem Presschieber häufig ab.

"Die Länge beträgt zwei Zoll, die Breite eine Linie.

"Er findet sich im Aland (*Cyprinus jesus*) nebst vielen Nelkenbindwürmern und Kratzern."

Batsch's drawings of the head are reproduced (Figs. 145, 146).

Prior to Batsch (1786) one other investigator reported cestodes of Cyprinidae which perhaps may be referred to this species. Bloch (1782:11) also had found this form in *Cyprinus*. He reported it under the descriptive name *Taenia articulis rotundis*. His report is inaccessible to me. Batsch knew of Bloch's report for he mentions it. Schrank (1788:49) reported this species under the name *Taenia orbicularis* and he mentioned *Taenia articulis rotundis* Bloch as a synonym. His diagnosis reads: "Vier Saugmündungen am Kopfe; die Glieder des Körpers tellerförmig. *Taenia orbicularis* . . . . . Wohnort, im Aland." Frölich (1791:58-61) described a cestode from *Cyprinus orfus* giving it the name *Taenia simplex*. This article is not accessible to me. Rudolphi (1802a:110-112) commented on Frölich's work on this form in these words: "Dass er (Frölich) Blochs *Taenia torulosa* nicht citirt, ist sehr begreiflich, da Bloch die Glieder ganz anders vorstellt. Ich glaube, dass die *Taenia simplex* nur jüngere Exemplare derselben Art bezeichnen." Gmelin (1790:3081) gave a brief diagnosis of *Taenia torulosa* which he credited to Batsch (1786) tho he also made reference to Bloch (1782). His diagnosis reads: "T. elongata torulosa, capite obtuso, collo crenato, articulis orbicularis: oculis geminis difformis, . . . . . Habitat

in Cyprino Jese, ad 2 pedes longa, capite plano, anterius truncato, collo brevi, articulis brevibus crassis."

Viborg (1795) reported *Taenia cyprini* idi upon which Rudolphi (1810:213) commented in these words: "*Taenia Cyprini* Idi. Viborg Ind. Mus. Vet. Hafn. p. 240. n. 133. T. Cyprini Idi.

"Non describitur, forsán tamen ad *Taeniam torulosam* (n. 22) pertinet, quae pluribus in Cyprinis occurrit."

Viborg's writings are not accessible to me. Dr. C. W. Stiles in reply to a letter asking for information on this species wrote, "Apparently Viborg mentions *Taenia idi* in 1795a (See author's Catalogue)," referring to the Index Catalogue of Medical and Veterinary Zoology. Zeder (1800:215, 220) reported a cestode from *Cyprinus* under the name *Rhytelminthus cyprini* which name he later (1803:352-3) considered to be a synonym of *Halysis torulosa*. His last diagnosis reads: "HALYSIS TORULOSA.—fere linearis, plana; capite terete, antice truncato, cum collo longo continuo; osculis anticis conicis; corpore crenato . . . . . Habitat in intestinis cyprinorum jesis et leucisci."

Rudolphi (1802a:110-12) after stating a brief diagnosis of *Taenia torulosa* presented some new data in the words which are here quoted:

"Ich habe diesen Wurm, wie Bloch, im Darmkanal des Alands, Cyprinus Jeses, im April, äusserst häufig angetroffen, aber nie über einen Fuss lang, da ihn Bloch hingegen doppelt so gross angetroffen hat. Der Kopf ist von Bloch gut beschrieben und abgebildet, die Saugwarzen und der ganz Kopf verändern ihre Gestalt alle Augenblicke, bald stehen ein paar Saugmündungen stark hervor, bald nur eine, bald alle; bald erscheinen sie wie tiefe Näpfschen, bald stehen sie hervor, bald sieht man sie zur Hälfte, bald ist der Rand gleichsam doppelt u. s. w. Uebrigens kann ich sie schon mit blossen Augen sehen; der Kopf ist bald mehr, bald weniger aufgeblasen, und immer stärker als der Hals. Der Körper ist rundlich und wird nach hinten allmählich grösser; dass er gegliedert ist, glaube ich gefunden zu haben, aber so deutlich ist er es nicht, wie man es auch nach der Blochschen Zeichnung (Taf. II. Fig. 1.) glauben sollte, wo man in einiger Entfernung vom Kopfe schon grosse runde Glieder wahrnimmt; bei den vielen von mir untersuchten Exemplaren nimmt der Körper in seinem Verlauf nur schwach zu, und die Glieder sind nur schwach unterschieden; auch habe ich an keinem einzigen eine Seitenöffnung bemerkt. Diese letztere findet man aber gewöhnlich nur bei grossen Exemplaren, und will ich also darin gerne Blochs Beobachtungen glauben."

Rudolphi (1810:111) gave a diagnosis, synonymy and description of this species which, because it admirably sums up all the previous work on the form and because of its inaccessibility, is here quoted verbatim:

"*Taenia torulosa* Batsch.—*Taenia*: capite truncato, osculis orbicularibus marginatis, collo mediocri, articulis crassiusculis (subquadratis) subrotundis.

Bloch Abh. p. 11. Tab. 2. fig. 1-4. *Taenia articulis rotundis*.

Batsch Bandw. p. 181 n. 27. fig. 105-108. *Taenia torulosa*.

Schrank Verz. p. 49. n. 150. *T. orbicularis*.

Gmel. Syst. n. p. 3081. n. 85. *T. torulosa*.

Frölich im Naturf. 25. p. 58-61. *T. 3.* fig. 4-6 *T. simplex*.

Zeder Nachtrag p. 220. *Rhytelminthus Cyprini*.

Rudolphi in Wied. Arch. 111. 1. p. 110. *Taenia torulosa*.

Zeder Naturg. p. 352. n. 39. *Halysis torulosa*.

"Hab. in ventriculo vel intestinis Cyprinorum. In *Cyprino Iese* Bloch et ego Aprili, in *Orfa* Frolichius eodem, in *Leucisco* Zederus Majo mense, reperimus.

"Descr. Vermes Zederiani septem ad novem lineas longi, dimidiam lati; Frolichiani duos ad quinque pollices longi, postice lineam lati; mei pedem non superantes vix lineam dimidiam lati; Blochiani duos pedes longi, lineam et quod excurrit lati.

"Caput truncatum, depressum, sub motu polymorphum, inflatum et *osculorum* directionem sum mopere mutans; haec circularia, concava, marginata, margine simplici vel duplici, interdum occultato; mox omnia quatuor, mox duo tantum in conspectum veniunt, ceterum oculis nudis usurpanda. *Collum* depressum, mediocre, a capite crassiore discretum. *Corpus* crassiusculum, subaequale, margine crenatum, articulis confluentibus, margine postico vix incumbentibus.

"Obs. 1. Blochius specimina sex maxima vidit, eorumque articulos quam in meis magis discretos, ovis farctos, et foramina marginalia (haec tamen non ulterius exposita, neque delineata) observavit. Frolichiani vermes a meis vix ulla nota differunt, nisi quod collum longum dicat, quod ipse mediocre, Blochius breve vocaverit, hoc autem vermis totius ratione habita facile explicatur; in vermibus enim bipedulibus collum vix pollicare Blochio breve visum, quod Frolichio in bivel quinquepollicaribus longum, mihi in pedalibus mediocre fuerit.

"Obs. 2. Zederiani vermes valde pusilli fuere, ideoque a nostra megis distant; ab osculis quatuor suctoriis totidem canales oriebantur, in corpore progressi, tandem in unicum vas abeuntes, quod in cauda obtuso-acuta terminabatur. Haec vasa mihi non visa, sed vermes illi tenelli plani, ideoque pellucidi fuere, nostri muto crassiores, fere teretiusculi. Zederus etiam postea ipse *Rhytelminthum cyprini* olim sibi dictum ad *T. torulosum* pertinere suspicatus est, quod olim in diario Wiedemanniano aequae indicaveram. Conf. etiam *Taeniam Cyprini* Idi n. 114. dictam."

Rudolphi (1819:150) stated that this species had been found by Bloch, Frölich, Zeder and himself in certain species of the Cyprinidae. Dujardin (1845:584) made no record of finding this species. He collected his data from descriptions by Zeder, Frölich, and Bloch. His description reads: "—Long de 16 à 20 mm, et large de 1.12 mm. (Zeder), ou large de 50 à 135 mm, et large de 225 mm (Froelich), ou long de 330 mm, large de 1.2 mm. (Rud.), ou enfin long de 660 mm, large de 225 à (?) (Bloch);—tête tronquée, de forme très-variable, ainsi que ses ventouses dont le bord est saillant;—trompe nulle;—cou de longueur médiocre;—articles assez épais, presque ronds."



Diesing (1850:514) found this species in *Leuciscus idus* and in *Alburnus bipunctatus* and further stated that Creplin found it in *Aspius rapax* and in *Alburnus* sp. Diesing's diagnosis added a little to the previous knowledge of the form. His diagnosis reads: "*Caput* latum depressum truncatum, acetabulis lateralibus limbo prominulo. *Collum* longum. *Articuli* teretiusculi subaequales longi confluentes. *Aperturae* genitalium. . . Longit. 7-10"; latit.  $\frac{1}{2}$ -1'". Van Beneden (1861:162-163) reported finding this form in several species of Cyprinidae ("plusieurs espèces de cyprins"). Altho he gave almost no descriptive data a comparison of his figures with those of Batsch leaves little doubt that his *Taenia porulosa* is identical and synonymous with *T. torulosa* Batsch. *Porulosa* probably is a misspelling of *torulosa*. Some authors have denied the synonymy of these names but their contention has no support of facts. Van Beneden failed to state the locality of his catch. Von Linstow (1878 and 1889) catalogued the hosts from which this species had been collected. He added nothing to the description of the species.

Zschokke (1884:20) stated that he found *Taenia torulosa* in *Coregonus fera*, *Lota vulgaris* and *Alburnus lucidus* from Lake Geneva. Since Zschokke reported *Taenia longicollis* and *T. ocellata* from *Coregonus fera* in addition to *Taenia torulosa* it is highly probable that all of his specimens from *Coregonus* belonged to one of the last named cestode species rather than to *T. torulosa*. Zschokke further states that his specimens were too young to permit him to recognize any trace of the internal organs. These statements as to a probable misdetermination of species apply equally well to his parasite report on *Lota vulgaris* in which case he found *Taenia ocellata* in addition to *Taenia torulosa*. His four young specimens from *Alburnus lucidus* may have been *Taenia torulosa* if only the question of host be considered. Of these four specimens he wrote: "La tête était large, tronquée, les ventouses très fortes et saillantes. Le cou était de longueur, médiocre, la segmentation en articles peu accusée." Lönnberg (1889:15) reported the finding of *Taenia torulosa* by Professor Tullberg. He gave no description and did not state the locality of the collection. Von Linstow (1891:565) found *Taenia torulosa* in *Alburnus lucidus*. He gave no data.

Krämer (1892:55) found *Taenia torulosa* in *Alburnus lucidus*, Lake Lucerne. He examined more than 150 specimens of *Coregonus fera* without finding a single specimen of *Taenia torulosa*, and among numerous specimens of *Alburnus lucidus* but a single host was infected with *Taenia torulosa*. He made the first careful morphological and histological study of this species. Lönnberg (1894:801-803) included *Taenia torulosa* in a list of species of his new genus *Ichthyotaenia*.

Zschokke (1896:775) found *Ichthyotaenia torulosa* (Batsch) in the intestine of *Leuciscus leuciscus* L. He found it in no other hosts. Von Rátz (1897:159) reported finding *Ichthyotaenia torulosa* in *Abramis brama* L. and in *Pelecus cultratus* L. in Lake Balaton, Hungary, but he gave no description. Frič and Vavra (1901:111-112) reported what they considered to be *Ichthyotaenia torulosa* (Batsch) (misspelling for *torulosa*) from *Leuciscus leuciscus* and *Perca fluviatilis*, Podiebrad, Bohemia. The description of their specimens agrees very well with that of *Proteocephalus percae* and a part or all of their specimens may belong to that species. The Häsling (*Leuciscus leuciscus*) would be a new host for *P. percae* and it may be that their specimens from that host are as they identified them, i. e., *P. torulosus*. Moreover, it is not impossible that Frič and Vavra failed to distinguish between the two species of cestode, *P. percae* and *P. torulosus*. It is impossible to make a complete determination from their data. Schneider (1902:24) found *Ichthyotaenia torulosa* in *Leuciscus idus* in Finland. Three years later he (1905:24-25) briefly but concisely described this species from *Leuciscus idus*. His description agrees very well with that of Krämer (1892).

Nufer (1905:75) reported *Proteocephalus torulosus* (Batsch) from *Perca fluviatilis*, *Alburnus lucidus*, *Squalius leuciscus*, *Blicca bjoerkna*, *Gobio fluviatilis*, *Coregonus exiguus albellus*, *C. schinzii helveticus*, *Salmo salvelinus*. Some of Nufer's report is open to doubt. In 59 specimens of *Perca fluviatilis* he not only failed to find the species which Zschokke found in that host but he found *P. longicollis* and *P. torulosus*, a species which only once before (Frič and Vavra, 1901) had been reported from that host. In that instance attention has been called to the fact that the specimens in question were probably *P. percae* and not *P. torulosus*. Nufer's *P. torulosus* and his *P. longicollis* may have been *P. percae*. Nufer's next four hosts after *Perca fluviatilis* are all Cyprinidae, from which group this species has heretofore been reported. It is extremely doubtful if the Salmonidae harbor this species. Zschokke, who in 1884 reported young specimens of *Taenia torulosa* from *Coregonus fera*, in 1896 found this parasite only in *Alburnus lucidus*. Zschokke's paper (1896) contained the results of his investigations on more than 1600 fish from Lake Geneva and the Rhine hence his data were fairly comprehensive. Moreover, from the three species of Salmonidae in which he claimed to have found *P. torulosus* Nufer reported two other species of *Proteocephalus*, namely, *P. longicollis* and *P. ocellatus*. Here again Nufer probably made a misdetermination. The writer has shown that Nufer's work (see discussion of *P. macrocephalus*) is untrustworthy and in the determination of this species there

seems to be no exception. That Nufer made a misdetermination of his *P. longicollis* is not at all improbable since specimens labelled "*Taenia longicollis* aus Forelle" which have been received by Professor Ward from Professor Zschokke have proved to belong to a different species. Nufer's tabulated description of *P. longicollis* (Nufer 1905:147) does not agree in some important points with von Linstow's description yet it is very manifest that he drew on von Linstow's description for a large part of his data. Likewise parts of Nufer's description of *P. torulosus* (Nufer 1905:147) fail to agree with the descriptions of that species by Schneider and Kraemer. Lühe (1909:32) gave a short specific description of this form under the name of *Ichthyotaenia torulosa* (Batsch). La Rue (1911:475) listed this form among other species of *Proteocephalus*.

The following study is based upon some of Schneider's specimens which Prof. H. B. Ward secured from Professor Levander at Helsingfors. This material is labelled "*Ichthyotaenia torulosa* Batsch. *Leuciscus idus*. Porkala. Juni 1901. det. G. Schneider." It now bears the number 10.121 in Professor Ward's collection. From this material frontal and transverse sections have been made and some heads have been studied in glycerine. A careful comparison of Schneider's (1905) and Kraemer's (1892) descriptions shows very good agreement. Zschokke's (1884) description in parts agrees pretty well with these two. Lühe (1909) seems to have based his specific description largely on the work of Zschokke, Krämer, and Schneider. Data from these sources are used in this description.

This is one of the larger species of *Proteocephalus* infesting fish. In length it varies from 65 to 600 mm. Specimens of the latter length are rare and have been reported only by some of the earlier investigators. The longest complete strobila examined by the writer was 110 mm. long. The breadth of the strobila varies from 1.2-2.25 mm. The head (Fig. 7) is large and very prominent, somewhat swollen in appearance, flattened dorso-ventrally, and somewhat flattened at the apex. Schneider found it 0.500 mm. broad. The heads in the writer's material measured 0.450-0.600 mm. broad by about 0.320 mm. thick. The suckers are very prominent, nearly circular in outline, with deep cavities and strong musculature. They are directed antieriad and a little outward. The suckers are 0.200 mm. in diameter according to Schneider and about 0.180-0.200 mm. in the heads examined by me. A fifth sucker is not present. In sections of the head the writer was unable to find even a trace of a vestigial fifth sucker. Nufer (1905:147) stated that the head of a 37 mm. specimen measured 0.255 mm. broad and the suckers of the same were 0.10 mm. in diameter. Nufer's measurements of the head do not



agree at all with the measurements made by Schneider or the writer. Neither Krämer nor Zschokke give measurements of the head and suckers but they state that the head is large, the suckers large and round. Nufer's specimens which infested *Perca fluviatilis* most certainly could not have been *P. torulosus* (Batsch) but were either *P. percae*, *P. fallax* La Rue, or an undescribed species.

Batsch drew the head of *P. torulosus* as a broad structure with large and prominent suckers. His figures which have been reproduced (Figs. 145, 146) should be compared with the drawing of a head (Fig. 7) derived from material sent to Professor Ward by Professor Levander. There is remarkable agreement in form of head and of suckers. The thick neck is about 2-3 mm. long by about 0.20-0.30 mm. broad. It is much wrinkled thus making difficult the determination of the length. It passes over gradually into the first proglottids which are much broader than long. Mature and ripe proglottids are almost always broader than long. The maximum length observed was 1.0 mm. and the maximum breadth 2.5 mm. Many nearly ripe proglottids measure about 0.29 mm. long by 1.30 mm. broad. The proglottids are thick and fleshy with well defined limits. Indentations between the proglottids are deep and the corners of the latter are quite pronounced. The end proglottid is rounded posteriorly. At its posterior end it has a deep indentation into which the excretory ducts discharge.

According to Krämer the excretory ducts in the head and neck region are very prominent with many anastomosing coils. In the neck region he found many branches of the excretory vessels leading to the exterior. Sections made by the writer failed to show these relations.

The genital openings are irregularly alternating, and are situated near the middle of the margin of the segment. The vagina opens not strictly anterior to the cirrus-pouch but somewhat dorsal thereto. Krämer incorrectly states that the vagina and cirrus-pouch open near each other but not into a common atrium. The testes are large, spheroidal or by pressure they may be sometimes rendered polyhedral. They measure according to Schneider about 0.160 mm. in sagittal by 0.080 mm. in frontal diameter. My measurements are about the same as these. The testes lie in two layers, the dorsal layer (Fig. 78) covering the entire area bounded by the vitellaria and the anterior and posterior margins of the proglottid. Thus the ovary is completely covered by the dorsal layer of testes about 70 in number. In the more ventral layer there are about 30-40 testes. Hence the total number of testes is about 100-110. Krämer's drawing (Fig. 184) shows a small number of testes but since it shows the ventral view of the worm it cannot show a large number. The coils of the vas deferens form a thick mass ex-

tending from the cirrus-pouch to the mid-field of the segment. Krämer (Fig. 184) figures the coils of vas deferens lying in the middle of the segment. The cirrus-pouch is short and relatively thick. Its length is about 0.255 mm. and its breadth 0.085 mm. The ratio of its length to the proglottid breadth is about 1:4 according to G. Schneider, 1:3 in Krämer's drawing, and 1:4-1:6 in my preparations. The cirrus is short and not very thick. Krämer's description of the cirrus is faulty in that he said that the cirrus was armed with recurved hooks which extend back into the tissue of the cirrus itself. There are no hooks. The protruded cirrus has not been seen by the writer. The ductus ejaculatorius forms but a very few coils or instead of coils it may lie in sinuous curves within the cirrus-pouch.

The vagina which opens mostly dorsal to the cirrus-pouch has a very weak sphincter muscle situated near the opening into the atrium. This sphincter vaginae is made up of a few strands of circular muscle fibers which may be easily overlooked. In its course to the interovarial space the vagina does not cross the cirrus-pouch but passes dorsal and anterior to the pouch. A small receptaculum seminis is present just anterior to the ovary. The vitellaria are lateral, voluminous, and follicular. The follicles are large and closely packed together. The bilobed ovary is large, well developed, thick and irregular in outline, but the lobes are not as slender as they are shown in Krämer's figure (compare Figs. 79 and 184). In proglottids 1.3 mm. broad the ovary may have a span of 0.80 mm. and the lobes may be 0.130-0.140 mm. thick. A muscular oöcapt and an oötype are present. The uterus in ripe proglottids has 3-4 lateral out-pocketings on either side. The uterine pores have not been observed. The eggs were not described by Krämer and Schneider. The outer membrane is thin and hyaline, 0.055 mm. in diameter. The granular second membrane has a diameter of about 0.032 mm. and the embryo about 0.021 mm. A delicate membrane closely invests the embryo.

*P. torulosus* differs from many other species of the genus by its large size, and from a large number of the species through its lack of a fifth sucker. In maximum length and breadth of its strobila it is the largest species of *Proteocephalus* yet described. In the width of the head and diameter of the suckers it is exceeded only by *P. ambloplitis* and *P. perplexus*. In observed length *P. torulosus* greatly exceeds these species—and it may be differentiated from them by its lesser number of uterine pouches, its weaker sphincter vaginae, its shorter cirrus-pouch, its double layer of testes, and by the arrangement of the dorsal layer of the same. It is greatly different from the other North American forms thus far described. Among the European forms *P. torulosus*

is approached in size only by *P. longicollis*. The latter, however, has a well developed fifth sucker and, according to von Linstow, a much smaller number of testes. *P. torulosus* may be differentiated from *P. percae* and *P. cernuae* by its larger head, larger suckers, lack of a fifth sucker, more numerous testes and the different arrangement of the same, and by its smaller number of uterine pouches. *P. torulosus* is much larger than *P. macrocephalus*. It has a larger head, larger suckers, fewer uterine pouches and a different arrangement of the dorsal layer of testes than the latter species. *P. torulosus* is so different from the other described species of *Proteocephalus* that a danger of its being confused with them is scarcely possible.

### PROTEOCEPHALUS MACROCEPHALUS (Creplin)

[Figs. 1, 47-49, 171]

1825:	<i>Taenia macrocephala</i>	Creplin	1825
1845:	<i>Taenia macrocephala</i>	Dujardin	1845:585
1850:	<i>Taenia macrocephala</i>	Diesing	1850:513-514
1859:	<i>Taenia macrocephala</i>	Molin	1859:13
1875:	<i>Taenia macrocephala</i>	von Linstow	1875
1889:	<i>Taenia dilatata</i>	Linton	1889:488-489
1893:	<i>Taenia macrocephala</i>	Olsson	1893
1896:	<i>Ichthyotaenia macrocephala</i>	Riggenbach	1896:267
1897:	<i>Taenia dilatata</i>	Linton	1897:425
1897:	<i>Taenia macrocephala</i>	Stossich	1897:7
1898:	<i>Taenia macrocephala</i>	Stossich	1898a:113-114
1898:	<i>Taenia macrocephala</i>	Mühling	1898:37, 69
1901:	<i>Taenia dilatata</i>	Linton	1901:435
1903:	<i>Ichthyotaenia hemisphaerica</i>	Schneider	1903:29
1905:	<i>Ichthyotaenia macrocephala</i>	Schneider	1905:10, 17-19
1905:	<i>Proteocephalus macrocephalus</i>	Nufer	1905:134-152
1909:	<i>Ichthyotaenia macrocephala</i>	Lühe	1909:33-34
1911:	<i>Proteocephalus macrocephalus</i>	La Rue	1911:475

**Specific Diagnosis:** The characters of the genus. Adult cestodes possessing strobila as much as 40 cm. long by 1-1.8 mm. broad or perhaps more. Segmentation quite distinct. Proglottids very numerous; first much broader than long; mature, broader than long or nearly quadrate; ripe, longer than broad. Neck 5.0-7.0 mm. long, 0.1-0.25 mm. broad. Head globose, flattened dorsoventrally, 0.28-0.30-0.32 mm. broad, 0.15-0.16 mm. thick. Suckers 0.095-0.106 mm. in diameter. Fifth



sucker vestigial and deeply set in the tissue of the head, 0.025 mm. in diameter. Sexual organs as in genus. Genital aperture marginal, near middle of proglottid. Vagina anterior and vaginal opening dorsal to cirrus-pouch. Testes 100-120, irregularly scattered between vitellaria, lying in one or two layers, usually one. Cirrus-pouch short, about 0.16 mm. long. Ratio of length of cirrus-pouch to proglottid breadth 1:6-1:8. Uterine pouches 7-11-12-14 on either side. Embryos 0.017-0.019-0.021 mm. in diameter.

Habitat: In intestine of *Anguilla vulgaris* (type host), and *A. chrysypa* Raf.

Host	Locality	Collector	Authority
<i>Anguilla vulgaris</i>	Greifswald (type locality)	Creplin	Creplin (1825:69-71)
" "	Rennes	Dujardin	Dujardin (1845:585)
" "	Padua	Molin	Molin (1859:13)
" "	.....	von Linstow	von Linstow (1875)
" "	.....	.....	Olsson (1893)
" "	Narenta	Stossich	Stossich (1897:7)
" "	Trieste	Stossich	Stossich (1898a:113-114)
" "	Memel, E. Prussia	Mühling	Mühling (1898:37-69)
" "	Finland	Schneider, G.	Schneider, G. (1903:29)
" "	Lake Lucerne	Nufer	Nufer (1905:134-152)
" <i>chrysypa</i> Raf.	Wood's Hole, Mass.	Linton	Linton (1889:488-489)
" "	" " "	Linton	Linton (1897:425-426)
" "	Sebago Lake, Me.	H. B. Ward	LaRue (the present paper)

Creplin (1825) found this species in the intestine of *Anguilla vulgaris* at Greifswald. His diagnosis and description are here given:

"*Taenia macrocephala*: T. capite elongato, antice crassiore, osculis globosis anticis, rostello brevissimo obtuso, collo brevi, articulis anterioribus brevibus obtusis, sequentibus subquadratis, horum lemniscis marginalibus vage alternis.

Hab. In intest. *Maraenae Anguillae* Martio, April, Majo et Junio hanc Taeniam reperi aut singulum aut minima tamen copia.

Descr. Vermes aliquot lineas usque ad octo pollices *longi*, majores medio corpore lineam cum quarta vel dimidia ejus parte lati, subdiaphani, albissimi.

Caput oblongum, antice latius, *rostello* brevissimo, obtuso instructum, inerme, et quatuor *osculis* (quorum orificia non vidi) globosis, prominentibus, anticis, instructum. *Collum* breve, rugosum, cum capite continuum. *Articuli* antichi brevissimi, inaequales, obtusi, passim medio constricti, sequentes sensim latitudine et longitudine crescunt, maximam partem quidem latiores, quam longi manent, de-

num vero quadrati et ultimi adeo paulo longiores, quam lati evadunt. Omnes per articulos decurrit ad margines laterales utrinque *linea alba opaca*. *Foramina* articulorum posticorum *marginalia* vage alterna, ex quibus cirrhus propendet brevis, subtilissimus.

Obs. 1. Reperi primo hujus vermis specimen unicum valde parvum d. 27 Mart. 1822, postea d. 23. Apr. ej. anni iterum parva specimina una cum Bothriocephalis clavaecipitibus itidem parvis demum vero specimen octopollicare d. 23. Maji 1822, et secundum specimen magnum d. 5. Junii 1823, simul cum illi adjacente Bothr. clavaecipite mediocre. Vivos examinae microscopii ope non mihi licuit, ut majorem descriptionis partem de verme in spiritu servato dare debuerim.

Obs. 2. Specimen Junio inventum vivacissimum, aquae frigidae immissum, valdopere se movebat et contorquebat, hisque motibus maximam *ovorum* copiam demittebat subglobosorum, ut tota aqua inde turbida fieret.

Obs. 3. Hujus vermis caput sine dubio O. F. Müller (Vid. Schriften Berl. Naturf. I. p. 208. cit. in *Rudolph*. Entozoologiae T. II. P. 2. p. 39.) vidit, cum Bothriocephalo clavaecipiti (Taeniae Anguillae sibi dicto, a nostra taenia omnibus notis diversissimo) caput osculis quattuor instructum adscriberet."

Dujardin (1845:585) reported and described specimens of this species in these words:

"Ténia de l'anguille. *Taenia macrocephala*.—Long de 8 à 220 mm, large de (?) à 3.37 mm;—tête allongée, plus épaisse en avant, avec une trompe très-courte, obtuse;—ventouses globuleuses, dirigées en avant;—cou court;—premiers articles courts, obtus, les suivant presque carrés, avec les orifices génitaux irrégulièrement alternes, et les pénis courts, très-minces, pendants.

"M. Creplin l'a trouvé plusieurs fois, à Greifswald, dans l'intestin de l'anguille.—J'ai trouvé aussi à Rennes, dans une anguille, trois jeunes ténias longs de 6 mm et 10 mm et 13.5 mm, larges de 0.25 mm à 0.3 mm; ayant la tête large de 0.33 mm à 0.48 mm, sans trompe, et les ventouses larges de 0.106, dirigées en avant."

Diesing (1850:513-514) added nothing to the earlier descriptions. Molin (1859) reported a specimen of this species taken from *Anguilla vulgaris* at Padua in March, 1859. He did not describe it. Von Linstow (1875) very insufficiently described *P. macrocephalus* from *Anguilla vulgaris* in the following words (The quotation is taken from Nufer 1905:135):

"Der Skolex ist gegen den folgenden Körper nicht abgesetzt; die vier grossen Saugnapfe haben einen Durchmesser von 0.166 mm.; dazwischen steht ein viel kleinerer, fünfter, scheitelständiger, von 0.026 mm. Durchmesser, der oft schwer aufzufinden ist. Die Cirren sind 0.2 mm. lang und 0.06 mm. breit; am äusseren Drittel zeigen sie eine Einschnürung, sodass ungefähr die Gestalt der Kegel entsteht, wie sie beim Kegelschieben üblich sind; sie ragen nur wenig mit der Spitze über den Rand des Gliedes hinaus und stehen unregelmässig abwechselnd.

Die äussere Eihülle ist hyalin und umgibt das Ei weitläufig, denn sie hat einen Durchmesser von 0.089 mm., während der der innern Eihülle nur 0.029 mm. und der der Eizelle selber 0.023 mm. beträgt. Die Embryonalhäkchen sind sehr fein; sie haben eine Länge von 0.006 mm."

Von Linstow's measurements of the suckers much exceed those given by Schneider and the writer for this species. He also reported a small fifth sucker that was very difficult to see. The writer is inclined to the belief that this was the small vestigial fifth sucker which in some *Proteocephalids* may be seen in favorable toto preparations.

Linton (1889:488-489) described some cestodes from *Anguilla chrysypa* Raf., caught on our eastern coast as a new species, *Taenia dilatata* in these words:

"Head small, truncate, or, in living specimens, slightly prominent in front. Acetabula nearly circular, directed a little forward. Neck rugose, very long, very contractile and dilatable, narrow in front, tapering toward the head; a short distance back of the head expanding into a number of irregular, transparent, dilated folds, which border both sides of an opaque central portion, in which two longitudinal canals are faintly outlined. First segments about three times as broad as long; median segments square, or broader than long; ultimate segments nearly square, sometimes broader than long, sometimes longer than broad. Genital apertures marginal, opening a very little in front of the middle.

"A single specimen of this species of *Taenia* was obtained from the intestine of the Common Eel (*Anguilla vulgaris*) August 26, 1885. The length of the specimen, when stretched out by fastening one end with a needle to the bottom of the dissecting dish and removing all kinks and curves with a fine brush, was 170 mm. The length of the same specimen, after having been preserved in alcohol, is less than 90 mm. The specimen when first obtained and placed in sea-water was quite active. The body was constantly throwing itself into sinuous curves, while the head and neck were jerked from side to side with a moderately rapid motion. In addition to these movements the neck and anterior portions of the body constantly changed their shape by the inflation or dilatation of the investing membranes into wide transparent folds, constricted at irregular intervals by narrow transverse bands. The neck, meanwhile, was alternately stretched out and contracted like the body of a Nemertean. The anterior end of the head protruded into a proboscis like papilla. The breadth of the head itself varied from 0.17 to 0.35 mm.

"In the alcoholic specimen the dilatable folds of the neck are much contracted and broken. They lie in rough, ragged frills along each side of the dark central part of the strobile. The head is truncate or blunt in front. The neck immediately behind the sucking-disks is almost as wide as the head, flat, thin, and little, if at all, tapering.

"The following measurements were made on the living specimen. The



head and neck changed their position and shape so rapidly that it was with the greatest difficulty that trustworthy measurements could be made:

	Millimeters.
"Breadth of head	0.28
Diameter of acetabula	0.12
Diameter of neck, narrowest part	0.20
Distance of first segments from head	17.00
Length of fourth segment from end of strobile	1.30
Breadth of same, posterior end	1.50
Breadth of same, anterior end	1.60
Length of posterior segment	0.90
Breadth of same, posterior end	0.60
Breadth of same, anterior end	1.25

"Habitat.—Common Eel (*Anguilla vulgaris*); intestine; Wood's Hole, Mass., August 26, 1885; one specimen."

"Von Linstow (Compend. der Helminth., 1878) records but two *Taenia* from the Common Eel, *T. macrocephala* Creplin and *T. hemispherica* Molin. *T. dilatata* is very different from the former. Diesing (Revis. der Ceph., Ab. Cycl., p. 378) mentions the latter, but gives no enumeration of characters. I do not have access to Molin's paper, and cannot, therefore say whether *T. dilatata* is identical with his species or not. The peculiar inflated character of the neck suggests *T. ambigua* Dujardin, but the difference in size between the adult specimens is alone sufficient to render the union in the same species impossible."

Again Linton (1897:425) reported this species from *A. chrysypa* thus:

"*Taenia dilatata* Linton.—No. 4812 U. S. N. M. From common eel (*Anguilla chrysypa*). Several strobiles but in bad state of preservation, no scolices; anterior ends have been exceedingly long and slender. The characteristic dilations of this species can not be proved from these specimens. The general appearance of the strobiles, as well as the character of the segments, however, agrees with this species.

"It may be added that the segments of these specimens agree with Molin's description of his *T. hemispherica*. With the evidence at hand, however, the writer does not feel justified in uniting the two species of *T. dilatata* and *T. hemispherica*."

Professor H. B. Ward secured this material, No. 4812, U. S. N. M. for my examination but its state of preservation was too poor to permit any positive determination being made.

Linton (1901:435) recording the parasites of *Anguilla chrysypa* reported this species again. "*Taenia dilatata* Linton. Specimens of this genus also taken in 1899, three on August 2. Dimensions in milli-

meters: Length, 8, diameter of head, 0.28. Diameter of sucker, 0.08. Segments not mature. One specimen August 28; length 14 mm."

It is the writer's opinion that the folds of the neck are of no real diagnostic value. Such folds may be seen on many other specimens of cestodes in certain states of expansion and contraction. Unfortunately Linton failed to figure or describe any of those internal structures which are of real service to the modern systematist. His drawing of the mature proglottid is such that it cannot be interpreted but his drawings of the head and of the last proglottids are of value for comparative purposes. Linton himself believed that the segments of his species agreed with Molin's description of *T. hemisphaerica*. Riggenbach (1896) considered Linton's *T. dilatata* to be identical specifically with *T. hemisphaerica* Molin. Nufer (1905) sought to show that these two species were identical with *Proteocephalus macrocephalus* (Creplin). This may prove to be the case but since the writer has not been able to study any material of the *T. hemisphaerica* he has preferred to consider the latter as a separate species. He is, however, ready to state that Linton's *Taenia dilatata* is specifically identical with *Proteocephalus macrocephalus* (Creplin). *T. dilatata* is therefore a synonym of the last named species and it should be dropped from the list of valid names for *Proteocephalus* species. Professor H. B. Ward very kindly secured for study Linton's slides and some alcoholic material of his *Taenia dilatata*. These specimens, judging from the statements in his letter to Professor Ward, must be from the lots described by Linton in 1889 and in 1901. Measurements of the heads, suckers, proglottids and the cirrus-pouch, together with the general appearance of the worms, give ample reason for considering this form to be identical with specimens taken from *Anguilla chrysypa*, Lake Sebago, Maine, and which the writer is describing as *P. macrocephalus*. These specimens agree in minute details of structure with the cestodes which Schneider (1905) described as *P. macrocephalus*. A more extended discussion of this comparison will be made in the proper connection (Vide infra).

Olsson (1893) reported specimens of cestodes from *Anguilla vulgaris* in Scandinavia. Riggenbach (1896) considered the form to be a species of *Ichthyotaenia*. Stossich (1897:7) reported this species from *Anguilla vulgaris* at Narenta, and again in a later paper (1898a:113-114) he gave a short diagnosis of specimens taken from the same host species at Trieste. In this diagnosis nothing of the inner anatomy of the worm is given. His diagnosis reads:

"Lunghezza 220 mm.; larghezza 3.5 mm. Scolice in continuazione del collo, allungato, ingressato all'innanzi, con grandi ventose globose, situate anteriormente; rostello cortissimo, ottuso, provveduto di una piccola ventosa apicale. Collo corto.

Proglottidi prime corte e ottuse, le seguenti subquadrate. Aperture genitali irregolarmente alterne; pene corto, sottilissimo, pendente, con una strozzatura verso l'apice. Uova con due invogli, lunghe 0.089 mm. Rara nell' intestino dell' *Anguilla vulgaris* (Trieste)."

Stossich was evidently describing *P. macrocephalus* and not the *P. hemisphaericus* (Molin). Mühling (1898:37, 69) noted this parasite in *A. vulgaris* in East Prussia but gave no description. Schneider (1903:29) reported from an eel a single specimen of what he then identified as *Ichthyotaenia hemisphaerica*. Later in a footnote (1905:10) he says of these specimens "*Ichthyotaenia hemisphaerica* kommt, wie es scheint, in den Aalen des Finnischen Meerbusens garnicht vor. Das Exemplar welches ich früher einmal irrthümlich als *I. hemisphaerica* bestimmt habe (Beiträge zur Kenntnis der Helminthenfauna des Finnischen Meerbusens. Acta Soc. pro Fauna et Flora Fennica 26, No. 3. 1903. S. 29), erwies sich bei genauerer Unterschung auch als *Ichthyotaenia macrocephala*."

From this statement the writer infers that Schneider at that time considered *P. hemisphaericus* to be a distinct species. In the text of the same article Schneider (1905:17-19) described *P. macrocephalus*, recording for the first time in the history of the species a careful study of its inner anatomy. For this reason a condensed resume of his description is here given.

*Proteocephalus macrocephalus*: This species is a close relative of *P. percae* and is differentiated therefrom by the very short cirrus-pouch and the short cirrus. The scolex has a diameter of about 0.30 mm. The diameter of the large deep suckers is 0.100 mm. The fifth sucker as in *P. percae* is a rudimentary structure made up of long cells and having a diameter of 0.025 mm. (The writer has shown that this organ in *P. percae* is a true sucker.) The neck is quite broad and is strongly compressed dorsoventrally. The body attains a length 40 cm. and more. A specimen 11 cm. long and 1.8 mm. broad had about 200 segments. The youngest proglottids are about five times as broad as long. The middle mature proglottids are broader than long while ripe proglottids are longer than broad.

The ovaries appear from the surface as two small stripes, as they do in *P. percae*. In old ripe proglottids they are of irregular shape, bent and somewhat overlapped. The cirrus and vagina open irregularly, alternating right and left, in the middle or a little anterior to the middle of the proglottid margin. The cirrus-sheath scarcely equals  $\frac{1}{6}$  the proglottid breadth, often much less. The ductus ejaculatorius (cirrus-canal) forms some convolutions in the proximal end of the cirrus-sheath and here widens out into a vesicula seminalis, 0.030 mm.



in diameter. The convolutions of the vas deferens outside of the cirrus-sheath are excentric on the porose side. In other species with a long cirrus-sheath this convoluted mass lies in the middle of the proglottid. The vagina is provided with a small sphincter muscle close to the vaginal opening. Without broadening out into a receptaculum seminis the vagina passes into the ovarial region. The oöcapt is very muscular. The uterine passage measures 0.02 mm. in diameter and the vitelline reservoir, 0.30 mm. The vitellaria are voluminous and follicular. The opening of the uterine passage and the well preformed uterine opening on the ventral side are found almost in the same transverse section posterior to the middle of the proglottid. The uterus has about eight branches on either side. Testes, numbering about 100 in each proglottid, lie irregularly in one or two layers. They measure about 0.150 by 0.075 mm. Ventral excretory vessels measure about 0.009 mm. in diameter, the dorsal vessels about 0.0025 mm. This species occurs only in *Anguilla vulgaris* and only in small numbers.

In this connection the writer thinks it of interest to note that Creplin's specimens were taken at Greifswald in Prussia while Schneider's were taken in Finland. Geographically these habitats are not distant nor do any barriers exist to prevent the movement of the eels from one locality to the other. For this reason and because of anatomical similarities it is extremely probable that Schneider's specimens were of the same species as Creplin's. It is to be noted that Dujardin's observations on the size of specimens taken from *Anguilla vulgaris* at Rennes, France, agree very well with those which Schneider describes. Nufer (1905) described and figured what he considered to be *P. macrocephala* (Creplin). He found two specimens in the intestinal tract of a single *Anguilla vulgaris* from Lake Lucerne. Nufer shows such striking inconsistencies in his statements and these agree so poorly with the findings of Schneider and the writer that it seems best to analyse parts of his paper. Compare his description of the head (Nufer 1905:137) and his statement about the head in his summary (Nufer 1905:145) with the facts presented in tabular form on pp. 146-147 of his paper where he compares *P. macrocephalus*, *P. ocellatus*, *P. longicollis*, and *P. torulosus*. All of these species he reports from Lake Lucerne.

He writes (page 137):

"Der Scolex ist sehr gross, ziemlich breit, rundlich, und besitzt einen Durchmesser von 0.1512 mm. Gegen den Hals ist er scharf und deutlich abgesetzt und übertrifft alle übrigen im Vierwaldstättersee vorkommenden *Proteocephalenscolices* an Grösse um Bedeutendes (The italics are mine, La Rue.); weshalb Creplin, auch auf den Gedanken gekommen sein mag, diesen *Proteocephalen* mit "*macrocephalus*" zu bezeichnen. Vorne ist der Skolex mit vier grossen, runden Saug-

näpfen versehen, die ihm die wuchtige Gestalt verliehen, wie ich sie sonst bei keinem *Proteocephalen* mehr angetroffen habe. Je nach der Kontraktion der Saugnäpfe erscheint ihr Rand kreisrund oder unregelmässig gelappt. Der äussere Durchmesser derselben beträgt 0.069 mm, der innere Durchmesser 0.0414 mm. Da der Skolex bei meinem Präparate etwas geschrumpft ist, war es mir unmöglich, einen fünften, scheitelständigen Saugnapf nachzuweisen, wie ihn von Linstow beobachtet haben will; jedoch ist sicher, dass eine Scheitelvertiefung vorhanden ist."

Also in his conclusions note this (p. 145): "Der Skolex übertrifft die übrigen *Proteocephalenskolices* an Grösse; dementsprechend ist auch der Durchmesser der Saugnäpfe grösser."

In the tabulated data (pp. 146-147) Nufer gives the dimensions of the scolices and of the suckers of the four species thus: breadth of scolex of *P. macrocephalus* 0.151 mm., *P. ocellatus* 0.114 mm., *P. longicollis* 0.43 mm., *P. torulosus* 0.255 mm.; diameter of suckers of *P. macrocephalus* 0.069 mm., *P. ocellatus* 0.05 mm., *P. longicollis* 0.12-0.19 mm., *P. torulosus* 0.1 mm. According to these figures the diameter of the suckers and the breadth of the head of *P. macrocephalus* exceed the same dimensions as given for *P. ocellatus* only. It is smaller than either of the other two with which he compares it.

Again note in the last sentence of the first paragraph quoted Nufer states that he could not find a fifth sucker, yet in his tabulated data (p. 146) he gives the diameter of the fifth sucker as 0.026 mm. In this he must be quoting from von Linstow's description. Von Linstow was the first to mention a fifth sucker for this species. Evidently Nufer's statements must lack accuracy. Nufer's drawings are of little help in giving a clear idea of the systematic position of his specimens.

Consider now his description of the male reproductive organs (pp. 140-142) and carefully compare his description with the writer's figure (Fig. 57).

"Der Cirrusbeutel ist keulenförmig; vorne an der Mündung schmal, erweitert er sich nach hinten ziemlich rasch und erhält einen grössten Durchmesser von 0.0945 mm. Am Hinterende ist er abgerundet und geht bis über die Mitte des Gliedes hinaus. Wie von Linstow (1875) am Cirrus, so beobachtete ich am äussern Drittel des Cirrusbeutels eine Einschnürung, durch die er ungefähr die von v. Linstow angegebene Gestalt eines Kegels erhält wie sie beim Kegelspiel üblich ist. Er dringt nicht vollkommen gerade in das Innere des Gliedes ein, sondern richtet sich etwas schräg gegen das Hinterende der Proglottids. Die Wandung des Cirrusbeutels wird von einer kräftig ausgebildeten Muskulatur umgeben. Ähnlich wie bei *Proteocephalus ocellatus* heften sich an die Basis des Cirrusbeutels kräftig entwickelte Retraktoren, welche die büschelige Wurzelfasern an einem Bulbus sitzen. Der Raum zwischen der Wandung des Cirrusbeutels und Cirrus ist von zarten Bindegewebszellen und zahlreichen, unregelmässig

verteilten Parenchymkernen erfüllt; vielleicht sind auch einzelne kleine Kalkkörperchen eingestreut, wie sie von Kraemer (1892) bei *Proteocephalus ocellatus* gefunden worden sind.

"Der Cirrus bildet die direkte Fortsetzung des Vas deferens; er durchbricht den Cirrusbeutel am Hinterende und durchzieht ihn in geradlinigem Verlaufe. Nachdem er den hintern Drittel des Beutels passiert hat, nimmt dessen Durchmesser ziemlich rasch ab und reduziert sich auf die Hälfte. Nach den Beobachtungen Kraemer's (1892) ist der Cirrus bei *Proteocephalus ocellatus* und *P. torulosus* in seinem hinteren Teile in mehrere Schlingen gelegt, während er bei *P. macrocephalus* als vollständig gestrecktes Organ auftritt. Gleichbedeutend wie diese Schlingen betrachte ich einige ringförmige wulstige Verdickungen am hintern Drittel des Cirrus. Der Schmarotzer besitzt in ihnen jedenfalls eine Einrichtung, welche, ähnlich wie der in Schlingen gelegte Cirrus, dazu dient, bei der Begattung den Cirrus zu verlängern. Bei dem Geschlechtakte würden dann die ringförmigen Wülste sich glätten und successive verschwinden in dem Masse, als der Cirrus vorgestossen wird. Er ist von einer strukturlosen, glatten Wandung umgeben, der nicht wie bei *P. ocellatus* und *P. torulosus* nach hinten gekrümmte Chitinhäkchen aufsitzen. Sein Lumen beträgt im hintern Drittel 0.009 mm., nimmt aber nach vorn bedeutend ab.

"Das Vas deferens liegt hinter und vor dem Cirrusbeutel etwas gegen den Seitenrand des Gliedes verlagert und bildet ein dichten Knauel, der sich besonders in der Länge der Proglottis ausdehnt; die Schlingen, die mit Samenfäden erfüllt sind, greifen kreuz und quer durcheinander. Die Wandung des Vas deferens ist viel zarter als diejenige des Cirrus und lässt keine besondere Muskulatur erkennen,

"Die Hoden liegen als grosse, rundliche Gebilde im Mittelfeld des Gliedes zwischen den Dotterstöcken, dem Keimstocke und dem vordern Gliedrande. Genauere Angaben über deren Zahl zu geben, ist wegen vorgerückter Reife der Glieder unmöglich; dagegen dürften sie ihres grossen Durchmessers (0.054 mm.) wegen kaum in grösserer Zahl auftreten. Bei *Proteocephalus ocellatus*, dessen Hodenbläschen beinahe gleichen Durchmesser (0.057 mm.) besitzen, fand Kraemer (1892) 27-30 in jeder Proglottis."

It will be noted that in nearly every particular his description agrees with the writer's drawing (Fig. 57) and with his description of the male organs of *P. fallax* La Rue, parasitic in *Coregonus fera*. The work of the writer on *P. fallax* was done on material from Zschokke's collection, and it seems that there can be no doubt that these specimens belong to the species described by Zschokke and Krämer as *Taenia ocellata* and by Nufer called *P. ocellatus* in his table. In the length and shape of the cirrus-pouch, in the position of the constriction of the pouch and in the inner bulbous end of the same Nufer's description and the writer's drawing (Fig. 57) agree well. The circular swollen thickening which he notes in the posterior third of the cirrus can be best interpreted to be a coil in the ductus ejaculatorius. When such a coil is seen under certain conditions the appearance described by Nufer is



simulated almost exactly. Likewise in the position of the mass of coils of the vas deferens, in the number, size and arrangement of the testes Nufer's description and his tabulated data (p. 146) agree very well with the writer's drawing and description of the same organs in *P. fallax* La Rue. His description of the male organs of the species in question cannot be said to agree with the writer's drawing (Fig. 49) which is a delineation of the proglottid of *P. macrocephalus*. Nor does his description agree with Schneider's or my own description of the proglottid of that species.

Unfortunately the writer has not had the opportunity of examining Nufer's material of this species nor any other specimens of cestodes taken from the eels of Lake Lucerne. He cannot therefore make a positive determination of Nufer's form. The evidence at hand permits several interpretations. These are: 1, that Nufer permitted his cestode material from *Anguilla* to become confused with specimens of *P. fallax* from *Coregonus fera*; 2, that the *Anguilla* of Lake Lucerne harbor *P. fallax*; 3, that the ripe proglottids described by Nufer had been taken into the intestine of the eel with its food, perhaps *Coregonus fera*, living or dead. Supposition 1 is always a possibility when one is working with such material. Supposition 2 does not give complete satisfaction because if the eels of Lake Lucerne harbor *P. fallax* Nufer ought to have been able to find a fifth sucker, which he failed to do. The third supposition permits one to consider that Nufer's whole specimens were really *P. macrocephalus* but that the ripe proglottids (in reality from *P. fallax*) upon which he based his description of the proglottids became confused with the specimens of *P. macrocephalus* by natural means. The embryo of Nufer's form is about the size of the embryo of *P. macrocephalus* as determined by the writer. His measurement of the embryo was 0.0184 mm. while the embryos of the writer's specimens of *P. macrocephalus* measured 0.017-0.019 mm. and rarely as much as 0.021 mm. in an elongated embryo. The embryo of *P. fallax* is much larger, according to the writer's measurements being 0.0312-0.0336 mm. in diameter.

Thus far attention has not been called to Nufer's description of the female generative organs. He claims that the histological structure of the vaginae of *P. macrocephalus* and of *P. ocellatus* differs in some respects. The writer's own investigation of the two species, especially when the investigations of Krämer are taken into consideration, lead him to believe that the vaginae of the two species are much alike in histological detail. Nufer describes the ovary as being single, not bilobed. In this he has been led astray by a condition sometimes found in ripe end-proglottids. In such cases the lobes of the ovary may be

pressed backward until the ends of the lobes touch in the median line. In the investigations of the writer covering a large number of *Proteocephalidae* he has been unable to find a fusion of the ovarian lobes. He must conclude that Nufer's drawing of this condition is hardly trustworthy. Nufer also claims that the walls of the uterine pouches eventually degenerate so that the eggs come to lie in the parenchyma. There is reason to doubt the accuracy of this statement. Many sections of a large number of old ripe proglottids of *P. macrocephalus* and other species of this genus have been examined by the writer who has failed to find any such degeneration of the uterine walls. Nufer's material must have been in extremely poor condition, or else he wofully misinterpreted the appearance of the sections.

The foregoing discussion of Nufer's article leads to the conclusion that the complete specimens taken by Nufer from *Anguilla vulgaris* were probably *P. macrocephalus*, as he identified them. One must further conclude that a part of his description was based on the two loose end-proglottids which really belonged to *P. fallax* and that these were ingested with the food of the eel or that they were accidentally put with the cestodes of *Anguilla* during Nufer's manipulation of the specimens. It also seems that the eggs which Nufer measured came from *P. macrocephalus*. Lühe (1909) gave a very short diagnosis of this form but included no figures of it. La Rue (1911:475) included this form in a list of *Proteocephalus* species and stated that *Taenia dilatata* was a synonym of *P. macrocephalus*.

Some specimens which have been identified by the writer as *P. macrocephalus* were collected by Professor H. B. Ward in the course of a biological investigation of Sebago Lake, Maine during the summer of 1907. This investigation was conducted under the auspices of the United States Fish Commission. Professor Ward examined 11 specimens of *Anguilla chrysypa* Raf. Of this number five had no cestode infection whatever; two yielded two *Proteocephalids* each; one yielded one *Proteocephalid*, and two others together yielded eighteen cestodes and some pieces. Of these eighteen cestodes eight were *Proteocephalids*. Some of the pieces also belonged to this group. Altogether then there were thirteen *Proteocephalids* plus some pieces but there was no complete strobila among them. The specimens described are from bottles No. 47, 54, 56, 71 and 72 of the Sebago Lake collection.

The worms are long and slender. No complete strobila was found but a fragment from the middle region of a worm measured 120 mm. long. The maximum breadth observed was 1.8 mm. Young proglottids are much broader than long, measuring 0.33 mm. broad by 0.022 mm. long. Mature proglottids are broader than long, measuring 1.0-1.20

mm. broad by 0.40-0.63 mm. long. The length of the ripe proglottids may exceed the breadth. They measure 0.90-2.08 mm. long by 0.491-1.20 mm. broad. The head (Fig. 1) is very short. It has a slightly rounded apex which is not marked by grooves or furrows. The head is somewhat flattened dorsoventrally, being 0.320 mm. broad at the base of the suckers and about 0.150-0.160 mm. thick. At or slightly above its broadest zone the head bears the four almost spherical suckers which have a maximum diameter of 0.095-0.106 mm. The opening of the sucker measures 0.050-0.060 mm. Tho not measured the sucker cavity is fairly deep. The musculature of the suckers is moderately well developed.

A fifth sucker is not present in this material, nor did Schneider or Nufer find one. It is replaced by a structure such as was described by the writer for *P. filaroides* and which was there called an endorgan. This structure is in reality a vestigial sucker. It has no elongated cells, tho Schneider says that he saw such cells, and there is no trace of muscels. In my specimens it is composed of a very few cells of irregular shape surrounded by a membrane that is homologous with a basal membrane in other suckers. This vestigial fifth sucker is situated a few micra below the cuticula and it has no connection with the exterior. It measures 0.020-0.025 mm. This structure does not resemble the fifth sucker of *P. percae* for it has been shown (Figs. 8, 9, 120) that in *P. percae* this is a muscular organ which doubtless functions as a sucker.

The neck is long and broad and thin. Frequently it measures 0.225-0.300 mm. or more in breadth while its length varies from 5.0 to 7.0 mm. The strobilation is quite evident. The notches between the segments are deep and the angles of the proglottids are somewhat rounded. Many shallow longitudinal folds give the surface of the worm a roughened appearance. The genital aperture is marginal, situated about the middle of the proglottid, and is irregularly alternating. There is no genital papilla. The excretory and nervous systems have not been carefully investigated. The musculature of the strobila is much as Benedict (1900) found it for *P. ambloplitis* tho the muscles are not as heavily developed.

The testes (Fig. 49) lie in a single layer in the dorsal region of the medullary parenchyma between the vitellaria and anterior to the ovary. They are closely packed together until many of them are more or less polygonal in shape. They measure 0.063-0.074 mm. long by 0.042-0.063 mm. broad and they number from 100 to 120. The vas deferens forms a thick mass of coils extending from the middle of the proglottid to the very short cirrus-pouch. Schneider very well says that the mass of coils of the vas deferens is excentric lying on the side in which the



cirrus-pouch is situated. The cirrus-pouch (Figs. 47, 48, 49) is very short, reaching just a little way through the vitellaria. Its length is about 0.160 mm. making the ratio of its length to the proglottid breadth about 1:6 to 1:8. The cirrus-pouch is bent up toward the inner dorsal wall of the dermo-muscular sac. Within the cirrus-pouch the ductus ejaculatorius forms but one or two coils before passing over into the short, but thick-walled cirrus. The cirrus is straight. It was not protruded in any specimens examined by the writer.

The vagina lies anterior to the cirrus-pouch, but the opening of the vagina into the genital atrium is situated almost dorsal to that of the cirrus (Fig. 48). Very near the opening of the vagina there is a weak sphincter vaginae. The lumen of the vagina in its initial region is quite large. This however soon constricts and the remainder of the vagina is of small diameter. The drawings (Figs. 47, 48) show how the vagina which opens anterior and dorsal to the cirrus-pouch passes over the latter in its course to the ventral surface and then backward to the ovary. Several species of *Proteocephalus*, e. g., *P. percae*, *P. pinguis*, and *P. exiguus* show this twisting of the vagina part way round the cirrus-pouch. This point has not been investigated in many species but it seems probable that it is quite a constant character of the genus.

The broadened region of the vagina bears a ciliated lining on its inner surface but the presence of the cilia could not be demonstrated throughout the length of the vagina. A small receptaculum seminis was found a little way anterior to the mid-piece of the ovary. The ovary (Fig. 49) is a heavy bilobed structure of much the same shape as in *P. percae* or *P. cernuae* tho shorter in those species. The vitellaria are long follicular masses in the lateral fields of the proglottids. The follicles are closely compacted. An oöcapt possessing a heavy musculature is present, also an oötype with its surrounding shellgland.

The uterus (Fig. 47) in ripe proglottids is made up of a median tube with 7-11-12-14 lateral outpocketings on either side. The septa between the uterine pouches are sometimes very thin and in other cases quite thick. The uterine passage is a small tube which after a sinuous course empties into the uterus about the middle of the proglottid. The uterine openings are 1-2 in number. Schneider in his specimens found only a single uterine pore. In reality this difference between the findings of Schneider and the writer is slight and too inadequate to serve as a basis for a specific distinction. A second uterine pore is very readily overlooked. Especially is this true in some species in which the second pore when present is smaller than the first and is situated some distance from it. The eggs were taken from the uterus of alcoholic specimens. The thin outer hyaline shell, characteristic of the eggs of

many species, could not be demonstrated. The outer shell, in this case corresponding to the second shell of most *Proteocephalus* species, was thick and quite granular. It measured 0.026-0.036 mm. in diameter, 0.026-0.029 mm. being the more common dimensions. The embryo, itself, varies from spherical to ovoidal. The diameter varies from 0.017 to 0.019 mm. and rarely 0.021 mm. for a long oval embryo.

The identity of this species with Linton's *T. dilatata* has already been discussed. Whether it is the same as *P. hemisphaericus* cannot now be determined. A discussion of its relationship to that form is given under the description of *P. hemisphaericus*. *Proteocephalus macrocephalus* shows no marked resemblances to any other of the North American species of *Proteocephalus*. In some respects it shows some marked resemblances to *P. cernuae* La Rue but it differs from that species in lacking a fifth sucker, in the possession of many more and larger testes, in having a cirrus-pouch that is much shorter actually and relatively, in having a much more voluminous mass of vas deferens and in having smaller embryos. The proportions of the proglottids are also different. While in some respects this species resembles *P. percae* its lack of a fifth sucker readily differentiates these two species. Moreover its very short cirrus-pouch is in marked contrast with the very long cirrus-pouch of *P. percae*. This species is very different from *P. torulosus* in size, in the arrangement of the testes, in the size of the cirrus-pouch and in the number of uterine pouches.

#### PROTEOCEPHALUS AMBLOPLITIS (Leidy)

[Figs. 18, 19, 116, 117, 134a & b, 183]

1887: <i>Taenia ambloplitis</i>	Leidy	1887:22-23
1887: <i>Taenia micropteri</i>	Leidy	1887:23
1896: <i>Ichthyotaenia ambloplitis</i>	Riggenbach	1896:267-268
1897: <i>Taenia ocellata</i>	Linton	1897:425-426
1900: <i>Proteocephalus ambloplitis</i>	Benedict	1900:339:355
1905: <i>Proteocephalus ambloplitis</i>	Marshall and Gilbert	1905:513-522
1909: <i>Proteocephalus sp.</i>	La Rue	1909:21, 25, 27, 28, 31, 36
1911: <i>Proteocephalus ambloplitis</i>	La Rue	1911:475

Specific Diagnosis: Characters of the genus. Cestodes large, 280-410 mm. long, 2-2.5 mm. in maximum breadth. Surface of body rough, with transverse and longitudinal furrows. Scolex prominent, 0.57-0.88 mm. broad, divided into quadrants by deep grooves. Tip of scolex usually marked by a minute depression with a slight elevation in the

center. Suckers large, round or oval in outline, deep, directed outward and anteriad. Length of suckers 0.300-0.400 mm. Fifth sucker vestigial, deeply embedded in tissue of head. Proglottids closely joined together, corners rounded. Young proglottids 12-15 times broader than long. Mature and ripe proglottids broader than long, about quadrate, or rarely longer than broad.

Genital sinus irregularly alternating, marginal, situated about end of first fourth of the proglottid. Vagina opening anterior to cirrus-pouch. Vaginal sphincter long and very thick. Receptaculum seminis present. Uterus with 15-20 lateral outpocketings on either side. Cirrus-pouch pyriform, muscular, 0.400-0.500-0.650 mm. long, reaching  $\frac{2}{7}$ - $\frac{2}{5}$  across the proglottid breadth. Cirrus, when protruded, long and slender. Ductus ejaculatorius much coiled. Vas deferens forming a great mass of coils extending to, or past, the middle of the proglottid. Testes 70-100 in number, situate between vitellaria. Eggs provided with three membranes. Outermost membrane hyaline, ellipsoidal, 0.036-0.043 mm. in diameter; second membrane thick, granular, 0.022-0.024 mm. in diameter; third closely investing the embryo; embryo 0.0168-0.018 mm. in diameter.

Habitat: Intestine of host.

Host	Locality	Collector	Authority
<i>Ambloplites rupestris</i> (type host)	Lake George, N. Y. (type locality)	Jos. Leidy	Leidy 1887:22-23
<i>Micropterus Salmoides</i> = <i>nigricans</i>	Lake George, N. Y. (type locality)	Jos. Leidy	Leidy 1887:23
<i>Ambloplites rupestris</i>	.....	J. W. Milner	Linton 1897:425-426
<i>Micropterus dolomieu</i>	Lake St. Clair, Mich.	H. B. Ward	Benedict 1900:339-355
<i>Micropterus dolomieu</i>	Lake Mendota, Wis.	Marshall & Gilbert	Marshall & Gilbert 1905:513-522
<i>Micropterus salmoides</i>	Walnut Lake, Mich.	T. L. Hankinson	La Rue (The present paper)
<i>Micropterus salmoides</i>	Pelican Lake, Minn.	E. G. Davis	La Rue (The present paper)
<i>Amia calva</i>	Lake Erie	H. B. Ward	La Rue (The present paper)
<i>Amia calva</i>	Lake St. Clair, Mich.	H. B. Ward	La Rue (The present paper)



This species was first described by Leidy (1887:22-23). His specimens were secured from the stomach of *Ambloplites rupestris*, Lake George, New York. His diagnosis reads:

"*Taenia Ambloplitis*.—Head quadrate, spheroidal, consisting almost entirely of the four large spherical bothria, with the summit slightly prominent and conical or depressed and unarmed; neck very short or none; body compressed cylindrical, gradually widening from the head to near the posterior part, where it slightly narrows to the end; segments linear, becoming gradually longer and wider, and the more quadrate, all deeply and pretty regularly wrinkled into two or three annuli. Genital apertures obscure. Length 8 to 12 inches; in alcohol contracted to  $3\frac{1}{2}$  to 5 inches; greatest width 2 mm.

"Head 0.5 to 0.625 mm. long and 0.75 to 0.875 broad. Bothria 0.375 mm. diameter. Commencement of body 0.625 wide. Anterior segments 0.125 long, 0.625 wide; subsequently 0.375 long and 1.5 to 1.875 wide; posterior segments 0.75 long by 1 mm. wide.

"A number of specimens from the stomach of the Rock Bass *Ambloplites rupestris*. Lake George, New York.

"This species resembles the *Taenia ocellata* Rudolphi of the European Perch, *Perca fluviatilis*, and perhaps is the same."

Leidy's drawings of the head and proglottids are reproduced (Figs. 134a and b). Immediately following his report on *Taenia ambloplitis* Leidy (1887:23) reported *Taenia micropteri* from the intestine of *Micropterus salmoides (nigricans)* Lake George, N. Y. in the following words:

"*Taenia Micropteri*.—Head large, compressed spheroidal, with four subterminal spherical bothria and a papilliform unarmed summit; neck none; body obscurely segmented, and with no obvious internal organs, posteriorly variably narrowed and obtusely rounded at the end. Length from half an inch to an inch, and about 1 mm. wide. Apparently a larval form; found in the body cavity of the Black Bass, *Micropterus nigricans*. Six worms, soft, white, and active. The longer ones of an inch would elongate to double the length, becoming proportionately narrower. The head, about 1 mm. or more in diameter, varied in length and breadth, according to contraction, sometimes one and sometimes the other being the larger. Lake George, N. Y."

This form is probably the larval form of *P. ambloplitis*. In dimensions and in general character the two forms are very much alike, even to the papilliform unarmed summit of the head. The obscure segmentation was probably due to wrinkling, not to a true segmentation. *P. ambloplitis* is the only adult Proteocephalid reported from *Micropterus dolomieu* and *M. salmoides* and it is known to occur in a closely related host species in the same lake in which Leidy found *Taenia micropteri*. This is additional evidence in support of the view that Leidy's species

are identical. In the light of the evidence the name *Taenia micropteri* is to be considered a synonym of *Taenia ambloplitis* and it should be stricken from the list of valid species because of the priority of the latter named species.

Riggenbach (1896:267-268) put this species in his list of *Ichthyotaenia* yet he considered it a doubtful form. Under the name *Taenia ocellata* Rud. Linton (1897) described this species from *Ambloplites rupestris*. His data agree very well with the data of Leidy, Benedict, and the writer. A difference in the length of the neck caused Linton to doubt the identity of his form with Leidy's *T. ambloplitis*. This difference is easily explained in forms so contractile and so wrinkled as these. Linton himself says, "My specimens agree with Doctor Leidy's pretty well except in the character of the neck. In *T. ambloplitis* the neck is described as 'short or none'. In my specimens the neck is long." Again in concluding Linton writes, "This reference of these *Taenia* of *Ambloplites* to the species *T. ocellata* is provisional only. I think, however, that there can be little doubt but that my specimens are identical with *T. ambloplitis* Leidy. The apparent absence of neck in Leidy's species may be ascribed to the presence of strong transverse wrinkles, due probably to the action of the preserving fluid." Benedict (1900:339-355) working in Dr. H. B. Ward's laboratory redescribed this species using Leidy's specimens for comparison with material which Professor Ward had collected from *Micropterus dolomieu* while engaged in a biological investigation of Lake St. Clair in August, 1893. Benedict by means of the section method demonstrated that, despite some discrepancies in size, his specimens and Leidy's agreed in anatomical and histological details. Marshall & Gilbert (1905:513-522) found this species in *Micropterus dolomieu* but not in other hosts from Lake Mendota, Wis.

La Rue (1909:21 et seq.) referred to a cestode found in *Micropterus salmoides* as *P. sp.* and in a footnote on the same page (p. 21) says, "This form may prove to be *Proteocephalus ambloplitis* Leidy, which it very much resembles". That species is now known to be *P. ambloplitis* Leidy. These specimens are referred to in the present article as No. TLH947 and No. TLH1036, collected by Hankinson. La Rue (1911:475) included this species in a list of species of *Proteocephalus*.

The following description of this species is based partly on Benedict's (1900) description and largely upon the writer's own work on material which Professor T. L. Hankinson had sent to Professor Ward for determination. This material was collected from the intestine of *Micropterus salmoides* in the course of a biological investigation of Walnut Lake, Michigan, summer of 1906. Other specimens have been

examined and identified as belonging to this species as follows: in unnumbered bottle, collection of La Rue, labelled "Black Bass, Large mouth, Pyloric Region, Pelican Lake Minn., 1909," collected by E. G. Davis; in bottle No. 10.151 labelled "Ex dogfish, Sandusky O. Jy. 7, 1905"; in bottle No. 2d labelled "7/10/01. P. in B. Host. *Amia calva*-Intestine"; in bottle No. 85 "7/12/01. P. in B. *Amia calva*. Intestine"; in bottle No. 295, "8/4/01. P. in B. *Amia*, Stomach." The abbreviation 'P. in B.' stands for Put-in-Bay, Ohio, the locality of collection. The bottles numbering 10.152, 2d, 85, 295 are in Professor Ward's collection. These together with the material collected by Hankinson were turned over to the writer for study through the kindness of Professor Ward.

This is one of the largest of the species of *Proteocephalus* and it is the largest species of that genus known at present from the fishes of North America. It may attain a length of 41 cm. and maximum breadth of 2.0-2.5 mm. The body is thick, fleshy and heavily muscled. In preserved specimens the outlines of the worm are somewhat rough, due to the furrows on the margins of the strobila. The surface of the worm is also rough. Longitudinal and transverse furrows are frequent. Especially noticeable is a deep median ventral furrow. On account of these furrows the strobilation is more or less indistinct. Likewise the posterior limit of the neck is frequently obscured by numerous transverse folds which give an appearance of segmentation.

The head is large and prominent. Its breadth is 0.75-0.875 mm. according to Leidy, 0.82-0.88 according to Benedict. The heads examined by me measured 0.57-0.60 mm. Benedict describes the shape of the head thus:

"From the anterior face it presents a nearly square outline, with a deep notch in the middle of each side, dividing the surface into quarters. Each quarter contains a large sucker which is directed outward and upward. The apex of the head is a smooth, rounded prominence with a small depression in the top. No hooks are present. A fairly good idea of the shape of the scolex can be obtained by placing two truncated pyramids base to base. One of the smaller bases will represent the beginning of the neck, the other the prominence, while on the slope just beneath this would lie the suckers. The notches seen in the anterior view of the scolex form furrows down the four sides of the head, which gradually decrease in depth and vanish on the first few proglottids."

Frequently the head is more globose than Benedict describes it. Such heads are figured (Figs. 18, 19). The small apical papilla may not always be seen but the furrows have been present in all heads examined by me. Leidy's figure of the head, reproduced (Fig. 134a), is somewhat similar to mine. It, however, does not show the furrows. Two of Benedict's figures of the head have been reproduced (Figs. 116, 117) for purposes of comparison.



The suckers which are deep and well muscled measure 0.30 mm. in length with a sucker opening of 0.150 mm. in my specimens. Leidy's measurement of the suckers was 0.375 mm. long and Benedict's was 0.32 mm. broad by 0.40 mm. long. In suckers of this size differences in contraction states will explain the variation in size. There is no functional fifth sucker but deep in the tissue of the head a peculiar structure (Fig. 116) may be found which is a vestigial fifth sucker. Benedict saw the structure but was unable to point out its significance. The neck is short and 0.25-0.45 mm. wide. The first proglottids are much broader than long measuring 0.344 mm. broad by 0.022-0.028 mm. long. Mature and ripe proglottids are broader than long as a rule, but at times may be quadrate, or even longer than broad. The last condition is rare. The maximum breadth of mature and ripe proglottids is 1.5-2.0-2.5 mm. while the maximum length of the same is 0.5-1.0-2.0 mm.

The cuticula, the musculature, and the nervous system were carefully investigated by Benedict (1900) who found nothing especially remarkable about these structures. The excretory system differs from that of *P. fossatus* (Rigg.) and *Corollabothrium lobosum* Rigg. in having no definitely placed foramina secundaria. At irregular intervals along either dorsal or ventral excretory vessel arise numerous branches which take a fairly direct course to the exterior. These branches are of various sizes and the lumen of each undergoes considerable variation in size in its course. The duct through the cuticula is very small and not beset with small bristles as Kraemer (1892) described for the species which he determined to be *P. filicollis*. No special musculature can be found in the course of these ducts to the exterior. The main longitudinal excretory vessels are four in number. They are situated just within the dermo-muscular sac. The ventral vessel has the larger lumen and it is further differentiated from the dorsal vessel by its very thin membranous lining. The dorsal vessel has a lining apparently made up of columnar epithelial cells. Rarely, however, the dorsal vessel is dilated to a size equalling that of the ventral vessel and in these cases the structure of the walls of the two vessels appears to be identical. No transverse vessel connecting the ventral or dorsal vessels in the posterior part of the proglottid has been found. In the scolex there is an intricate plexus of excretory vessels. Many ducts opening to the exterior by small pores place the coils of this plexus in communication with the exterior.

The common marginal genital sinus opens about one fourth of the length of the proglottid from the anterior end. It is irregularly alternate in position. A genital papilla is not present. The vagina opens into the sinus anterior to the cirrus-pouch. The testes are spheroidal bodies,

0.050-0.065 mm. in diameter, which are sometimes rendered polyhedral by pressure of adjacent testes. They number from 75 to 100 and are crowded into one or two irregular layers in the space between the vitellaria and anterior to the ovaries. The vas deferens (Fig. 183) forms a large mass of coils beginning in the mid-field of the proglottid and reaching to the cirrus-pouch. A large part of this mass of vas deferens is posterior to the cirrus-pouch. The cirrus-pouch (Fig. 183) is a large pyriform structure, heavily muscled with both longitudinal and circular muscles. Its larger and inner end is attached by heavy muscle strands to the dermo-muscular sac. It measures 0.40-0.50-0.65 mm. long by 0.150-0.230 mm. in maximum breadth. The ratio of its length to the proglottid breadth varies from 2:7 to 2:5. When it is protruded the cirrus is long and slender, a little larger at the base than at the tip but when within the cirrus-pouch the basal part of the cirrus has a broad lumen. This sharply defines the cirrus from the slender ductus ejaculatorius which forms an intricate mass of coils.

The vagina (Fig. 183) always lies anterior to the cirrus-pouch. Very near its opening the vagina dilates markedly and in this region it is provided with a thick and powerful sphincter vaginae measuring about 0.030 mm. thick by 0.300 mm. long. This prominent sphincter surrounding the greatly dilated vagina renders the latter a striking feature of the proglottid and makes a valuable diagnostic character for the species. At the inner limits of the sphincter the vagina contracts sharply and beyond the constriction it again dilates. Here its inner surface is weakly ciliated. Anterior to the ovary the vagina may describe a few coils before it passes into that portion of its length which is differentiated into a small receptaculum seminis. Entering the inter-ovarial space the vagina describes a few coils and then discharges into the oviduct. The ovary (Fig. 184) is situated in the posterior part of the proglottid. It is bilobed, each lobe being thick, broad and somewhat club-shaped. The lobes extend laterad to the vitellaria. From the mid-piece of the ovary arises a muscular organ, the oöcapt or gulping organ. From the oöcapt arises the oviduct which after making one or more coils is joined by the vagina. From this point the oviduct extends to the oötype. Just as it enters the oötype the oviduct receives the common vitelline duct which has been formed by the union of the paired vitelline ducts arising in the posterior part of the vitellaria.

The oötype is surrounded by the so-called shell-glands, the individual cells of which are long and clubshaped. The oötype discharges into a somewhat muscular duct known as the uterine passage which extends anteriad passing the ovary on the dorsal side. It discharges into the uterus from the dorsal side of the latter at a point about 0.080-0.110

mm. anterior to the ovary. Benedict (1900) stated that there was no uterine passage in this species. An examination, however, of his slides and reconstruction drawings convinced the writer that a uterine passage was present in Benedict's specimens as it was in his own. The vitellaria are lateral and follicular. In this species they do not extend posterior to the lobes of the ovary nor do they parallel the posterior margin of the proglottid. The uterus in young proglottids is a median ventral tube from which later 15-20 lateral outpocketings develop on either side. Benedict's drawing reproduced (Fig. 183) shows but a part of the pouches. There are 1-2-3 preformed uterine pores. The uterine eggs are covered with three membranes, an outer, thin hyaline, a middle thick and granular membrane and an inner thin membrane closely investing the embryo. The outer membrane which is not spheroidal but ellipsoidal measures about 0.036-0.043 mm. in length. The middle shell is spherical 0.022-0.024 mm. in diameter. The embryo measures 0.0168-0.017 mm. in diameter.

The American forms which most resemble this species are *P. perplexus* LaRue and *P. nematosoma* (Leidy). The latter may be the same as *P. ambloplitis*. *P. perplexus*, however, is distinguished from *P. ambloplitis* by its smaller head, smaller suckers, thinner and smaller strobila, by the smaller size and the different location of its sphincter vaginae, by the posterior prolongation of its vitellaria, by its much smaller cirrus-pouch, by its fewer coils of ductus ejaculatorius, by its larger number of testes, and by the smaller size of the eggs. *P. ambloplitis* greatly resembles *P. nematosoma*. It differs from that species chiefly in the somewhat larger size of the head and suckers. *P. ambloplitis* is larger than most of the old world species of *Proteocephalus* and it differs from a large number of these in not possessing a fifth sucker. It resembles *P. torulosus* in the lack of a functional fifth sucker and in size. It may be easily differentiated from *P. torulosus* by reason of its larger head and suckers, by its sphincter vaginae which for size and length is unique in the genus, by its more numerous uterine pouches, and by the different arrangement of testes.

*P. ambloplitis* may be distinguished from all other known species of *Proteocephalus* by means of its extremely large sphincter vaginae which because of its length and its extraordinary development is remarkable. This species is also readily distinguished from all other species of the genus by reason of the large number of coils of the ductus ejaculatorius.



## PROTEOCEPHALUS PERPLEXUS La Rue

[Figs. 17, 64, 65]

- ? 1886: *Taenia filicollis* Leidy, 1886:62-63.  
1911: *Proteocephalus perplexus* La Rue, 1911:478-479.

Specific Diagnosis: The characters of the genus. Observed length as much as 15.5 cm. Maximum breadth 1.7 mm. Strobilation evident. Angles of proglottids sharp and distinct. First proglottids much broader than long. Mature proglottids broader than long, 1.70 mm. broad by 0.595 mm. long. Ripe proglottids quadrate or longer than broad, 1.02 mm. broad by 1.10 mm. long to 1.75 mm. long by 0.510 mm. broad. Head somewhat spheroidal, flattened dorsoventrally, divided into four quadrants by grooves extending nearly to the apex. At apex frequently a small papilla situated in a small depression. Head 0.663-0.714 mm. broad, 0.425-0.510 mm. long. Suckers four, 0.340-0.459 mm. long by 0.255-0.272 mm. broad. Cavity of sucker deep. No fifth sucker, no rostellum. Neck broad and thick, about 0.5 mm. long.

Genital pore marginal, situated at end of first fourth or half of proglottid, irregularly alternating. No genital papilla. Cirrus-pouch elongated oval in shape, 0.30-0.344 mm. long, extending  $\frac{1}{3}$ - $\frac{1}{4}$ - $\frac{1}{5}$  across the proglottid. Ductus ejaculatorius with 1-3 coils. Cirrus when protruded spindle-shaped, slender, thicker at base, 0.60 mm. long. Testes 135-155 in number, in one layer occupying dorsal field between vitellaria anterior to ovary. Testes 0.069 by 0.037 mm. in diameter. Vagina anterior to cirrus-pouch, never crossing same, beginning region dilated. Inner surface of vagina heavily ciliated. Vitellaria follicular, voluminous, follicles of same large, compacted. Portion of vitellaria paralleling posterior margin of proglottid. Ovarian lobes thick, heavy, irregular. Uterus, when developed, possessing 20-25 lateral pouches. Uterine pores 2-4. Uterine eggs provided with three membranes. Inner and outer membranes thin, second thick, granular, sometimes partially or wholly split into two layers. Embryos 0.013-0.014 mm. by 0.014-0.0156 mm., second membrane 0.019-0.030 mm., outer membrane 0.024-0.036 mm. in diameter.

Habitat: In intestine of host.

Host	Locality	Collector	Authority
<i>Amia calva</i> L. (type host)	Illinois river, Havana, Ill. (type locality)	H. B. Ward	La Rue (Present paper)
? <i>Amia calva</i> L.	North Carolina	Jos. Leidy	La Rue (Present paper)
<i>Lepisosteus</i> <i>platostomus</i>	Illinois river	H. B. Ward	La Rue (Present paper)

Type: Alcoholics No. Ha89a and slides from the same lot. Co-types:—Ha 10 a; Ha 10 e; Ha 29 a; Ha 30 h; Ha 77 a, b, e; Ha 94 e, h, and slides of Ha 94 h, in Dr. H. B. Ward's Collection.

Leidy (1886:62-63) found some specimens of a cestode in *Amia calva* from North Carolina. These specimens, he thought, might be *Taenia filicollis* Rud. His specimens, judging from his data probably belong to the species *P. perplexus* but since Leidy published no drawings of his specimens no positive determination can be made. That part of his report containing his data is here quoted:

"The worms accorded with the description of the *Taenia filicollis*, infesting Sticklebacks, *Gasterosteus*, and is probably the same species. They range from 1½ to 3 inches long, gradually widening from the delicate thread-like neck to the posterior rounded extremity, where they measure from 1 to 1.5 mm. wide. The head is spheroidal, variably broader or longer, and about 0.625 mm., with the summit slightly prominent and unarmed and with four hemispherical, lateral bothria 0.25 mm. in diameter. Neck variable, when extended long and narrow and usually about half the width of the head. Anterior segments, transversely linear, about an eighth the length of the breadth, gradually becoming inverted saucer-shaped or scutellate, and about one-fourth the length of the breadth. Posterior segments more quadrate, slightly widening behind, about 0.75 mm. long and from 1 to 1.5 mm. broad; last segment longest and rounded. Genital apertures marginal."

La Rue (1911:478-479) briefly described this species and gave it the name *Proteocephalus perplexus*. The specimens upon which this species is based were collected at Havana, Ill., June and July 1910, by Dr. H. B. Ward. The hosts *Amia calva* and *Lepisosteus platostomus* were caught in the Illinois river at that place. Four *Amia* were examined, three were infested with 30, 10 and 15-20 specimens of *P. perplexus* respectively. One was uninfested. Eight gars were examined; three were infested with 6, 3 and 5 specimens of *P. perplexus* respectively. Five of the gars were not infested with this species. In all the *Amia*

and in one of the infested gars the *P. perplexus* was not accompanied by any other species of *Proteocephalus*. In two of the gars *P. singularis* occurred together with *P. perplexus*. Nothing is known regarding the seasonal distribution of the parasite and almost nothing regarding its geographical distribution. It has not been found in the *Amia* of the Great Lakes which Professor Ward examined a number of years ago. In those specimens were found *P. ambloplitis*.

Judging from external appearances alone these specimens of *P. perplexus* are very much like specimens of *P. ambloplitis*. Even after staining and mounting some pieces in toto they appear to belong to that species tho certain points of difference may be indistinctly made out. Examination of sections revealed certain characters by which the two species may be differentiated. The writer (1911:478) proposed the name *Proteocephalus perplexus* for this species by reason of the difficulties attending its differentiation from its nearest congener. In size *P. perplexus* is somewhat smaller than *P. ambloplitis*. Its strobila is shorter, narrower and thinner. Its head is a little smaller than that of *P. ambloplitis* but is very similar in shape and it has four grooves as does that species. Sometimes the minute papilla at the apex of the head thought to be characteristic of *P. ambloplitis* may be seen. The suckers are large and in a position similar to that which they occupy in *P. ambloplitis*.

The head (Fig. 17) is somewhat spheroidal. It is flattened dorso-ventrally and is evenly rounded anteriorly. Four grooves extend from the base of the head nearly to the apex where frequently there is a small papilla in a shallow depression. The head is not as truncate as the head of *P. ambloplitis* described by Benedict (1900). It resembles very closely heads which the writer has examined and drawn (Figs. 18, 19) of the latter species. Four heads of *P. perplexus* measured in breadth and length 0.663 by 0.510 mm., 0.697 by 0.425 mm., 0.697 by 0.510 mm., 0.714 by 0.459 mm. The suckers measured 0.340-0.459 mm. long by 0.255-0.272 mm. broad. There is no fifth sucker and no rostellum. Sections through the apex of the head failed to reveal even a vestige of a fifth sucker. In *P. ambloplitis* the rudimentary fifth sucker is large. The suckers are deep and well muscled, usually longer than broad. The sucker-opening is directed outward and slightly forward. The neck is 0.5-0.6 mm. long. It is broad and thick but narrower than the head. No complete strobila was found yet most of the longer pieces contained ripe proglottids. Six pieces with heads measured 65, 91, 106, 105, 125, and 155 mm. long respectively. The maximum breadth observed was 1.7 mm.



The worm shows a very evident strobilation, the angles of the proglottids being sharp and well marked. The posterior border of one proglottid overlaps the anterior end of the one following. Segmentation begins about 0.5-0.6 mm. from the head. Here the segments are much broader than long. Gradually the length increases in proportion to the breadth until in nearly mature proglottids the dimensions may be 1.70 mm. broad by 0.595 mm. long. Further down the strobila nearly ripe proglottids may be about quadrate 1.02 mm. broad by 1.10 mm. long. Ripe proglottids are longer than broad, 1.75 mm. long by 0.510 mm. broad. In all but ripe proglottids the genital pore is not prominent but in these long proglottids the pore is situated on an eminence. Moreover in this part of the strobila the posterior region of the segment is much broader than the anterior or middle region. The neck is 0.5-0.6 mm. long. It is broad and thick, not as broad, however, as the head.

The genital pore is situated on the lateral margin at the end of the first one-fourth to one-half of the proglottid. The pores alternate irregularly. In mature and nearly ripe proglottids there is no genital papilla but in elongated ripe proglottids a genital prominence is noted. Into the common genital sinus both vagina and cirrus open, the vagina always anterior to the cirrus. The male organs (Fig. 65) much resemble the male organs of *P. ambloplitis* but here again certain differences exist. The cirrus-pouch in *P. perplexus* is not as voluminous nor as long as in *P. ambloplitis*. It measures 0.300-0.344 mm. long. Its length goes into the proglottid breadth 3-4-5 times depending somewhat upon the state of contraction of the proglottid. Within the cirrus-pouch are 1-3 coils of ductus ejaculatorius, a much smaller number than in *P. ambloplitis*. The coils of the vas deferens outside the cirrus-pouch are very numerous. They form in mature proglottids a thick compact mass extending from the cirrus-pouch to the middle of the segment. The cirrus itself is well muscled. When protruded it is a long spindle-shaped organ slightly thicker near the base than elsewhere. It is nearly 0.60 mm. long. The testes are very numerous, 135-155 in number. They are arranged in one layer, occupying the entire dorsal field anterior to the ovaries and as far laterad as the vitellaria, with the exception of the small region taken up by a portion of the cirrus-pouch and the vas deferens. The testes measure as much as 0.069 mm. long by 0.037 mm. broad, their short axis lying parallel to the long axis of the worm.

The vagina (Fig. 64) in its first part is considerably dilated. Throughout the full length of this dilated region there is a weak circular musculature. At the end of the dilatation is a strong sphincter vaginae 0.053 mm. long and 0.015 mm. thick. *P. ambloplitis* has a long

and extremely heavy sphincter vaginae while in *P. singularis* the sphincter vaginae resembles that of *P. perplexus*. Throughout its length as far as the receptaculum seminis the inner surface of the vagina is heavily ciliated. The vagina does not cross the cirrus-pouch, but after reaching the mid-field of the segment it takes a sinuous course posteriad to the interovarial space. A small receptaculum seminis lies just anterior or posterior to the mid-piece of the ovary. The vagina forms no coils anterior to the ovary. The vitellaria (Fig. 64) are voluminous, the follicles are of good size and closely packed together. They extend not only to the extreme posterior margin of the proglottid but are bent around and lie parallel to the posterior margin nearly to the mid-field. This is particularly noticeable in ripe proglottids. The paired vitelline ducts pass through this posterior continuation of the vitellaria.

The ovary is bilobed. The lobes are thick and heavy, with a somewhat irregular outline due to protuberances. In sections it is noted that the ovary is not a solid organ but is made up of smaller parts more or less fused together. An oöcapt, oötype, shell gland and other organs usually found in the inter-ovarial space in Proteocephalids are found here and in the relations characteristic of the genus. The uterus (Fig. 64), a median tube in mature proglottids, is made up in ripening proglottids of a median tube and 20-25 narrow lateral pouches. These pouches occupy the entire ventral field between the vitellaria and the anterior and posterior proglottid limits. There are 2-4 ventral uterine pores. The uterine eggs have three membranes, an inner one closely investing the embryo, a middle membrane, quite thick and granular and frequently partially or completely split into two layers, and an outer membrane thin and hyaline. The embryo measures 0.013-0.014 mm. by 0.014-0.0156 mm., being usually somewhat elongated but at times spheroidal. The second membrane measures 0.019-0.030 mm. and the outer one 0.024-0.036 mm. in diameter.

The excretory system is made up of four main lateral canals which traverse the length of the strobila. The two ventral vessels are larger than the two dorsal. At intervals small branches arise from the main vessels and lead to the exterior. No transverse excretory commissure was observed. In the head and neck the anastomoses of the excretory system are very complex. The main trunks are nearly straight.

This species is closely allied to *P. ambloplitis* yet it differs from that species in size, in the lack of a vestigial fifth sucker, in the size and location of the vaginal sphincter, in the posterior prolongation of the vitellaria, in the smaller cirrus-pouch, in the fewer coils of ductus ejaculatorius within the cirrus-pouch, in the greater number of testes and

in the size of the eggs. In size *P. perplexus* somewhat resembles *P. singularis*. It also resembles *P. singularis* in the shape and proportions of its proglottids and in the character of the vagina and vaginal sphincter. These two species differ in the size and shape of the head, suckers, and neck. Tho nearly of the same size the strobila of *P. perplexus* is the larger. *P. perplexus* has more numerous testes, a larger cirrus-pouch and more numerous coils of ductus ejaculatorius. The main excretory vessels of *P. perplexus* are straight, but they are very sinuous in *P. singularis*. *P. perplexus* differs from all the European species in the position of the sphincter vaginae and in the extension of the vitellaria along the posterior border of the proglottid.

### PROTEOCEPHALUS SINGULARIS La Rue

[Figs. 24, 25, 39-41, 83-87]

1911: *Proteocephalus singularis* La Rue, 1911:479

Specific Diagnosis: Characters of the genus. Strobila long and slender. Observed length up to 170 mm., length probably as much as 250 mm. in complete individuals. Maximum breadth up to 0.90-1.0 mm. Head small, 0.250-0.30 mm. broad by 0.20-0.22 mm. long. Head bearing at broadest part four large suckers. Apical region of head frequently prolonged into an unarmed rostellum-like organ. Deep grooves between suckers. Suckers of variable shape, always with pointed apex, with shallow cavity and thin muscular wall. Length of suckers 0.130-0.170 mm., breadth of same 0.170-0.190 mm. No fifth sucker, no vestige of same. Neck slender, 2.0-3.0 mm. long by 0.1-0.2 mm. broad. First proglottids broader than long, 0.255 mm. broad by 0.017-0.020 mm. long. Mature proglottids as much as 0.85 mm. broad by 0.34-0.37 mm. long. Ripe proglottids longer than broad or quadrate 0.680 mm. broad by 0.90-1.00 mm. long. Old spent proglottids up to 2.0 mm. long by 0.4 mm. broad. Segmentation evident. Posterior angles of proglottids slightly projecting.

No genital papilla. Genital pore marginal, irregularly alternating, situated at end of first  $\frac{1}{4}$ - $\frac{1}{2}$  of proglottid. Testes numerous, 75-80 or 90, in a single layer occupying entire field between vitellaria anterior to ovary. Breadth of testes 0.4-0.6 mm., length of same 0.07-0.10 mm. Vas deferens a large mass of coils in the mid-field. Ductus ejaculatorius with few or no coils. Cirrus slender, straight, muscular. Cirrus-pouch slender, nearly straight, muscular, 0.185-0.20-0.265 mm. long. Length of cirrus-pouch  $2\frac{1}{2}$ -3 times into proglottid width.



Vagina always anterior to cirrus-pouch, never crossing the latter. Beginning region of vagina narrow. This region about 0.1 mm. long, terminated by weak sphincter vaginae. Adjacent to narrow region a dilated portion. Vagina not ciliated in any part of length. Vesicula seminalis present. Vitellaria with large follicles, not paralleling posterior margin of proglottid. Uterus when fully developed with 20-25 lateral outpocketings on either side. Uterine pores ventral, 2-3-4 in number. Eggs with three membranes. Embryos 0.014-0.0156-0.0168 mm., second membrane 0.026-0.031 mm., outer membrane 0.027-0.033 mm. in diameter. Excretory system has four main lateral trunks. Ventral vessels large, dorsal vessels much smaller. All main vessels sinuous or spiral. Many secondary openings to exterior.

Habitat: In intestine of *Lepisosteus platostomus* (type host), Illinois river, Havana, Illinois (type locality).

Type: Alcoholics No. Ha 30 i and slides from same. *Cotypes*, Ha 12 d, e; Ha 29 f; Ha 87 a; Ha 88 a; Ha 101b; Ha 110c. Material in Dr. H. B. Ward's collection.

La Rue (1911:479) in a preliminary way described this species.

In a collection of endoparasites secured by Dr. H. B. Ward from fish caught in the Illinois river at Havana, Illinois, were some specimens of *Proteocephalus* somewhat resembling the species which the writer (1911) has designated as *P. perplexus*. On account of the peculiar form of the head and suckers of this species the name *Proteocephalus singularis* La Rue has been proposed for it. In all, eight gars were examined. Of this number only one was uninfested with this parasite. This gar was infested only with *P. perplexus*. The numbers of *P. singularis* present in each of the seven infected hosts were: 2, 7, 26, 2, 5, 4, 8. Two gars had a mixed infection of *P. singularis* and *P. perplexus*. Slides have been prepared from some of this material.

Its study showed that the longest piece measured 170 mm. Complete strobilas perhaps measure up to 250 mm. or more. Its maximum breadth is about 0.90-1.00 mm. The strobila is slightly smaller than that of *P. perplexus* yet it greatly resembles the latter species in outward appearance. The more slender neck and the smaller head are its more readily noted points of difference. The head (Figs. 24, 25) is small, measuring from 0.250 to nearly 0.300 mm. in breadth by 0.20-0.22 in length. At its broadest part it bears four large suckers which when well expanded cover up nearly the whole surface of the head except the apical region. The apical region in most species is flattened or conical, but in this species it is drawn out into a long slender protuberance which has no hooks. This is not a rostellum. At times this

protuberance is greatly contracted. Between the suckers are deep grooves which in many cases cause the head to appear almost lobate. The suckers themselves are more or less variable in shape but they always show the pointed apex. The cavity is shallow, the muscular wall thin. The suckers measure 0.130-0.170 mm. long by 0.170-0.190 mm. broad. A fifth sucker is not present. A careful search through three series of sections has failed to reveal any trace of an endorgan. The neck is long and slender, 2.0-3.0 mm. to the first traces of segmentation. The breadth is 0.1-0.2 mm., usually much narrower than the head. The neck grades over almost imperceptibly into the first proglottids which are very difficult to discern.

The first proglottids are 12-15 times broader than long, being about 0.255 mm. broad by 0.017-0.020 mm. long. As the proglottids near maturity they increase greatly in size measuring up to 0.85 mm. broad by 0.34-0.37 mm. long. Proglottids in which the uterus contains some eggs measure 0.51 mm. long by 0.867 mm. broad or are even quadrate, each dimension being about 0.85 mm. The ripest proglottids become longer than broad, measuring 0.680 mm. broad by 0.90-1.00 mm. long and in rare cases of old spent proglottids the length may be about 2.0 mm. and the breadth about 0.4 mm. Segmentation is evident. No longitudinal furrows are present. Transverse furrows occur only at the division lines between the segments. The posterior angles of the proglottids project slightly beyond the anterior margin of the proglottid following.

This species has not been thoroly investigated as to its histological structure. However, certain points have been worked out with some care. The cuticula, the subcuticula, the parenchyma, the muscles of the strobila, and the nervous system were not seen to differ essentially from similar structures in *P. ambloplitis*.

The muscles of the head were worked out in series of transverse and frontal sections. The muscles of the apical protuberance of the head could not be worked out with care but that region could be seen to be well supplied with muscles especially in the subcuticular layer. The peripheral parts of the apical region of the head contain many heavy muscles going up toward the tip. In the middle and lower region of the suckers about 0.135 mm. from the tip of the head heavy muscles cross from one sucker wall to the wall of the sucker opposite forming a heavy muscle cross (Fig. 40). Weaker muscles cross the head dorso-ventrally and laterally. These muscles extend to the subcuticular region and serve by their contraction to cause in part the deep grooves between the suckers. Near the upper limits of the suckers at a depth of about 0.10 mm. from the tip of the head heavy muscles (Fig. 39)

connect the sucker wall with the lateral or dorso-ventral surfaces of the head. These probably serve a double function of causing by their contraction the deep grooves between the suckers and of pulling the adjacent margins of the suckers together, thus broadly flaring the sucker. In this region the muscle-cross is weakly developed. In the lower part of the head (Fig. 41) just as the suckers disappear from transverse sections the fibers of the muscle-cross flare out to secure a broad attachment on the sucker wall. In fact a great many fibers dip down below and attach themselves near the lower outer margin of the sucker. At the sides of each sucker large groups of very heavy muscles may be found the attachments and courses of which are best made out in longitudinal sections. Transverse fibers, i. e. lateral and dorsoventral, pass through the muscle-cross and assist in the formation of a muscle-star (Fig. 41). Below this point the muscles rapidly assume the relations of the muscles in the strobila.

The longitudinal muscles of the head are fairly well worked out. Certain groups which were of undetermined character in transverse sections can be readily distinguished in frontal sections. The large groups of tangentially cut ends (Fig. 41) at either side of the sucker are in reality longitudinal muscles which come up from the neck region and find their attachment on either side of the sucker (Fig. 87), right and left. Much weaker muscle bands pass up toward the tip of the scolex. In the apical region (Fig. 86) many heavy muscles attached to the sucker wall pass out by diverging paths to the subcuticular area. These probably control not only a certain part of the movement of the suckers but also the form of the apex. The muscles of the head, both longitudinal and transverse, are much more strongly developed than in the head of *P. filaroides*, which the writer has worked out with great care (La Rue 1910). Their arrangement in the two forms is very similar, tho certain groups of muscles present in *P. singularis* are lacking in *P. filaroides*.

In the head the excretory vessel may be followed as coiling and anastomosing trunks and vessels which are much less developed than in *P. ambloplitis* or *P. perplexus*. In the neck region the anastomoses of the excretory system are much like those in the head. Here four main lateral vessels are to be found with branches which have a very few openings to the exterior. A little further posteriad the excretory vessels increase in size. This is particularly true of the ventral vessel. Both ventral and dorsal vessels have a very sinuous or spiral course even in the most elongated proglottids. In frontal sections (Fig. 83) the sinuous ventral vessels appear as series of oval or circular spaces in the parenchyma. In either frontal or transverse sections the ventral



vessel is very prominent on account of its very large lumen. At frequent intervals branches may be seen to be given off from the ventral vessel and a lesser number from the dorsal. Many of the ventral branches communicate to the exterior by means of small ducts through the cuticula. These branches are more numerous and more prominent than in any other *Proteocephalid* examined by the writer. One branch opens quite regularly at the posterior angle of the proglottid. Other branches (by far the largest number) open on the ventral surface. A few branches of the ventral vessel open on the dorsal surface. No duct connecting the ventral excretory ducts in the posterior part of the proglottids has been observed, nor have the relations of the excretory vessels been observed in the end-proglottid.

There is no genital papilla. The genital pore is marginal, irregularly alternating, and situated at the end of the first third or two-fifths of the proglottid. Vagina and cirrus open into the common genital sinus, the vagina always anterior to the cirrus. In all the general features of the sexual organs these are typical of the genus. The testes are ovoidal or spheroidal in shape, 0.04-0.06 mm. broad by 0.07-0.10 mm. long. They are arranged (Fig. 85) in a single layer which fills the dorsal region between the vitellaria anterior to the ovaries. The region in which the coils of the vas deferens lie is free from them. They are 75 to 85-90 in number. The vasa efferentia can very readily be made out just below the layer of longitudinal muscles of the dorsal side. These empty into the vas deferens which makes a large mass of coils in the middle of the proglottid and reaching over to the cirrus-pouch. This knot is relatively thick for it extends from dorsal to ventral wall of the dermo-muscular sac. Entering the cirrus-pouch (Fig. 84) the vas deferens which now becomes the ductus ejaculatorius passes over almost immediately into the straight cirrus. The ductus ejaculatorius is usually straight but sometimes it is thrown into from one to three small coils. The cirrus itself has not been seen protruded. It is always slender, straight, and muscular. The cirrus-pouch (Fig. 84) is slender, nearly straight, and quite muscular. It measures 0.185-0.200-0.265 mm. long. Its length goes  $2\frac{1}{2}$ -3 times into the proglottid width.

The vagina (Fig. 84) in its first part has a narrow lumen. This region extends about 0.100-0.110 mm. from the vaginal opening. It is characterized by its rich covering of gland cells and its weak longitudinal and circular muscles. The vaginal sphincter which is poorly developed is situated just at the end of this first region. The sphincter is about 0.025 mm. long. Immediately following this region with the narrow lumen is a dilated portion which may extend clear to the vesicula seminalis. There is no ciliated region of the vagina. The vagina

does not cross the cirrus-pouch but lies anterior thereto until it comes to the knot of the vas deferens which it passes ventrally. It forms no coils anterior to the ovary but may be somewhat sinuous. The vitellaria (Fig. 85) are lateral. The follicles are large, and closely packed together. In the posterior part of the segment the vitellaria never extend posterior to the ovary as in *P. perplexus*. The vitelline ducts are as in *P. ambloplitis*. The lobes of the ovary are smaller than in *P. perplexus* or *P. ambloplitis*. They are more branched than in either of those species but this branched condition cannot be determined except in sections.

The relations of the oöcapt, oötype, oviduct, lower vagina, vitelline ducts, and uterine passage are typical of the genus and need no explanation here. The uterus is a median tube in mature proglottids. In ripe proglottids (Fig. 83) the median tube has 20-25 lateral outpocketings on either side which take up the entire ventral field of the segment bounded by the anterior and posterior margins and by the ventral excretory ducts. Two, three or four ventral uterine pores have been observed, tho in most of the very old proglottids the ventral body wall is split from end to end. The formation of the ventral uterine openings is as La Rue (1909) described the process in *O. filaroides*. The eggs very much resemble those of *P. perplexus* in size but differ in having a thinner and more hyaline middle membrane which is never split into two layers. The embryos measure 0.014-0.0156-0.0168 mm. The second membrane measures 0.026-0.031 mm. and the other hyaline membrane 0.027-0.033 mm.

This species in the structure of the head stands quite by itself. Its proglottids somewhat resemble those of *P. perplexus* but are smaller. In toto preparations the ventral excretory ducts of *P. singularis* being much larger make a fairly easy means of separation. In the number of uterine pouches the two species are much alike, but these pouches in *P. perplexus* extend farther laterad than in *P. singularis*. In the position of the vaginal sphincter the two species are much alike but the beginning region of one is dilated, in the other contracted. One has a ciliated vagina, the other not. The cirrus-pouch of *P. singularis* is more slender, the cirrus and ductus ejaculatorius are straighter and more slender than in *P. perplexus*.

## PROTEOCEPHALUS SULCATUS (Klaptocz)

[Figs. 130, 131, 175, 176]

1906:	<i>Ichthyotaenia sulcata</i>	Klaptocz	1906:123-130
1911:	<i>Proteocephalus sulcatus</i>	La Rue	1911:475

**Specific Diagnosis:** The characters of the genus. Cestodes of small size, up to 68 mm. long. Maximum breadth 1.5-2.0 mm. Scolex very variable in form, unarmed, without apical depression or fifth sucker, divided by distinct furrows into four quadrants. Median furrows arise near first proglottids. Cross-section of one type of scolex nearly round, of the other elliptical. Breadth of scolex 0.46-1.75 mm., thickness of same 0.67-1.28 mm. depending on contraction states. Suckers, deep rounded, one in each quadrant. Diameter of sucker 0.250 mm. Neck none. First proglottids broader than long. Mature and ripe proglottids quadrate or longer than broad. Last proglottid rounded posteriorly. Maximum breadth of proglottid 1.5 mm., maximum length of same 2.0 mm.

Genital pore at end of first third of segment. Cirrus-pouch about 0.20-0.25 mm. long, extending about  $\frac{1}{4}$  across the proglottid. Several coils of ductus ejaculatorius in cirrus-pouch. Cirrus when protruded long and slender. Testes about 200, irregularly arranged between vitellaria. Opening of vagina posterior to the cirrus-pouch. Lumen of vagina large. Ovary posterior, bilobed. Vitellaria follicular, lateral. Uterus with 10-12 lateral out-pocketings in ripe proglottids. Eggs pear-shaped, circular in cross-section. Diameter of same 0.016 mm, length up to 0.019 mm.

**Habitat:** *Polypterus endlicheri* Heckel (type host), taken at Duem (type locality) on the White Nile, and *Clarotes laticeps* Rüppell, from the White Nile in the region of Khartoum.

The material was collected by Dr. F. Werner in the spring of 1905, was described by Klaptocz (1906), and was listed by La Rue (1911) among other species of *Proteocephalus*. In the summary and also in the following description the data are taken from Klaptocz's paper and from his drawings.

A specimen from *Clarotes* measured 68 mm., one from *Polypterus* 60 mm. The scolex (Figs. 130, 131) is of very variable form, is unarmed, has no apical depression, and it always shows four very distinct furrows of which the two on the median line are the heavier. These divide the anterior face of the scolex into four large similar quadrants whose acute angles come together at the tip of the scolex. The free



margins of the quadrants often are indented especially on the flattened sides. The furrows, especially the heavier median ones, arise in the region of the first proglottids. In each quadrant a deep rounded sucker is sunken which lies nearer the margin of the scolex than to its tip. Two types of scolex are recognized with intermediate forms. The one is more or less flattened on the anterior face. It has a more or less round cross section. Its furrows are shallow, and its suckers are directed anteriorly while the other type has an elliptical transverse section. Its thickness is less than the breadth of the scolex. The scolex itself is much flattened. The furrows are deep and very plain, reaching nearly to the tip of the scolex. The suckers are more elongated and the sucker openings are directed outward. These types of head are to be considered contraction states of the same species since intermediate stages are present. The second type is found in *Polypterus*, and the first type in *Clarotes*. The diameter of the scolex in specimens from *Clarotes laticeps* ranges up to 1.72 mm, the diameter of a sucker of the same 0.250 mm. The diameter of the smallest scolex of this host is 0.75 mm. The thickness of scolices from *Polypterus endlicheri* ranges from 0.67 to 1.28 mm., the breadth from 0.46 to 0.675 mm. No neck is present. The youngest proglottids are thinner than the head and only slightly narrower. Their breadth exceeds their length. Proglottids increase in both breadth and length with age until they are quadrate in form or longer than broad. The last proglottid is rounded posteriorly. The maximum breadth of a proglottid from *Clarotes* is 1.5 mm, maximum length 2.0 mm. The maximum breadth of a segment from *Polypterus* is 1.5 mm. and the maximum length of the same 1.9 mm.

Sexual ripeness appears very early. The anlagen of genital organs in stained specimens may be seen in very young proglottids within two scolex lengths of the head. Many proglottids are sexually ripe before becoming quadrate in form. The marginal genital pore alternates irregularly. Sometimes in as many as ten to twelve or more proglottids the genital sinus may be on the same side tho this condition is rarely true in more than five segments. The sinus (Fig. 176) is situated at about the end of the first third of the segment. The vagina opens posterior to the cirrus-pouch. The cirrus-sheath (Fig. 176) containing the coiled cirrus (or cirrus plus the ductus ejaculatorius) has a pear-shaped form and lies perpendicular to the margin of the proglottid. It may extend  $\frac{1}{4}$  across the breadth of the proglottid. The cirrus-pouch is about 0.20-0.25 mm. long (measured from Klapotcz's figures which are drawn to scale). The cirrus (Fig. 176) when protruded is very long and slender. It is thicker at the base than at the point and is devoid of hooks or bristles. The testes are elliptical, in number about 200. The testicular

field is limited by the vitellaria, the anterior margin of the segment and the ovaries. There is no median zone free from them except where they are pushed aside by the developing uterus. As the uterus continues to develop the testes are pushed well into the lateral fields.

The vagina (Fig. 176) which has a large lumen runs to the middle of the proglottid in a more or less sinuous course, then bends and passes directly back to the posterior end of the segment. In proglottids with developed uterus the vagina is pushed somewhat from the median line and, it seems, always toward the side on which it opens. The ovary is posterior, is bilobed, and the lobes are limited laterally by the vitellaria. In the end-proglottid the lobes of the ovary are bent together. The vitellaria are follicular and lateral. On the porose side the vitellaria is divided into two parts connected by small follicles which lie dorsal and ventral to the genital passages. The uterus (Figs. 175, 176) is a median tube reaching to the anterior end of the proglottid from which arise many (10-12 in drawing) lateral outpocketings. These are separated when fully developed by thin tissue-layers. The eggs are pear-shaped, circular in cross-section, 0.016 mm. in diameter and 0.029 mm. long.

Despite the fact that Klaptocz found an apparently intergrading series between the types of head mentioned by him it seems to the writer that there is a possibility of his having confused two forms of very similar appearance. The writer in the present work on *Proteocephalus perplexus* and *P. ambloplitis* found considerable difficulty in distinguishing the heads. And in certain respects the structure of the internal organs of the proglottids was remarkably similar. So too it was found to be difficult to distinguish the proglottids of *P. perplexus* and *P. singularis*. This was made especially difficult when both species occurred in a specimen of *Lepisosteus platostomus*. The fact that this species seems to occur in two such widely separated families of fish is a further intimation that two species of parasite are here included under the one name. Material from the two hosts should be carefully reworked.

## PROTEOCEPHALUS PENTASTOMA (Klaptocz)

[Figs. 126-129]

1906:	<i>Ichthyotaenia pentastoma</i>	Klaptocz	1906:130-133
1911:	<i>Proteocephalus pentastomus</i>	La Rue	1911:475

Specific Diagnosis: Characters of the genus. Cestodes of small size. Strobila up to 28 mm. long; maximum breadth of same 1.19 mm. Neck none. First proglottids many times broader than long. Mid-proglottids 1.19 mm. broad, 0.21 mm. long. Sixth from last proglottid 0.59 mm. broad, 0.21 mm. long. Head large, oval in cross-section, 0.975 mm. broad by 0.83 mm. thick. No rostellum, no hooks. Four large suckers, oval or round in outline, 0.50 mm. in diameter, situated in four quadrants. Suckers separated from each other by longitudinal furrows. A true fifth sucker 0.085-0.100 mm. in diameter situated at apex of head. Genital aperture about middle of proglottid. Vagina posterior to the cirrus-pouch. Testes 70-100, arranged irregularly between vitellaria with tendency toward formation of two lateral fields. No data on cirrus-pouch and vas deferens. Vitellaria lateral, not voluminous. Ovary bilobed, posterior. Uterus immature.

Habitat: *Polypterus bichir* Geoffr., White Nile near Khor Attar.

Klaptocz (1906) described this species and it has not since been described from the specimens. La Rue (1911:475) gave it a place in a list of species of *Proteocephalus*. A single specimen was taken by Dr. F. Werner, Feb. 16, 1905, while making a journey up the Nile river into the Sudan. All data are taken from Klaptocz's (1906) paper since it was impossible to secure any material for the writer's examination.

Measurements of the worm are as follows: Total length 28.0 mm.; lateral diameter of scolex 0.975 mm., dorso-ventral diameter 0.83 mm.; maximum diameter of suckers 0.5 mm.; diameter of fifth sucker 0.085-0.10 mm.; thickness of proglottids near scolex 0.46 mm., breadth 0.87 mm., length 0.04 mm.; maximum breadth of proglottid near middle of the strobila 1.19 mm., length 0.21 mm.; breadth of sixth proglottid from end 0.59 mm., length 0.21 mm.; breadth of next to last proglottid 0.41 mm., length 0.31 mm.; breadth of last proglottid 0.33 mm., length 0.51 mm. The scolex (Figs. 126, 127) is somewhat oval in transection, surpassing the breadth of the first proglottids. It possesses no rostellum, no armature of hooks, but has an apical sucker 0.085-0.100 mm. in diameter. The four equal sized suckers of somewhat oval or round shape vary in size in different individuals. They are about 0.50 mm. in



diameter and are situated on the four quadrants of the head. The four quadrants are somewhat swollen and are separated from each other by longitudinal furrows. The apical depression is a true sucker, as is shown in the stained specimen. There is no neck, the first segments appearing under the microscope 0.060 mm. behind the margin of the suckers. The size relations of the proglottids have already been given. From the drawing, reproduced (Figs. 128, 129), the strobilation is evident, the posterior angles of the proglottids being quite prominent.

The anlagen of the sexual organs may be seen 7 mm. back of the tip of the scolex while the well developed testes may be seen 3 mm. farther posteriad. These are elliptical in shape, their long axis lying in the long axis of the worm. They number 70-100, and lie irregularly scattered between the vitellaria and anterior to the ovaries. They are most numerous in the lateral fields but they may also occur in the median part especially in the anterior region. No data are given concerning the cirrus-pouch and the vas deferens. The genital pore is irregularly alternating. It is situated near the middle of the margin of the segment, but in the last proglottids a trifle anterior thereto.

The vagina opens posterior to the cirrus-pouch. Just before its opening it possesses a considerable broadening, the diameter of which is about equal to the broadest diameter of the cirrus-pouch. On either side of this broadened part the vagina is narrow. The vitellaria are lateral longitudinal glands which develop late. They are not voluminous. The bi-lobed ovary lies in the posterior part of the proglottid as in *Proteocephalids*. Since the uterus was immature in this species the eggs could not be observed.

This species easily separates itself from the most of the forms, parasitic in fish, by reason of the large size of its head and suckers. The position of the vagina posterior to the cirrus-pouch is a further diagnostic character of value, while the lack of an unsegmented neck and the proportions of the proglottids are characters which serve for its identification. Unfortunately Klaptoetz failed to describe and to figure the cirrus-pouch, cirrus, and vas deferens which are of great value in making a positive determination. The uterus being immature could not be described. For these reasons this species which probably is a species of *Proteocephalus* cannot be accurately placed in its relation to the other members of the genus.

## PROTEOCEPHALUS FOSSATUS (Riggenbach)

[Figs. 133, 180]

1896:	<i>Ichthyotaenia fossata</i>	Riggenbach	1896:166-193
1911:	<i>Proteocephalus fossatus</i>	La Rue	1911:475

Specific Diagnosis: The characters of the genus. Cestodes of short length, 3.5-4 cm. long. Scolex large, visible to naked eye, maximum breadth of same 0.714 mm. Anterior end of scolex conical, bearing at apex a slight concavity, not a fifth sucker. Suckers, round, 0.34 mm. in diameter, borne at broadest part of head. Neck broad, 0.85 mm. long. First proglottids broader than long, 0.612 mm. broad by 0.135 mm. long. Mature and ripe proglottids, quadrate to longer than broad. End-proglottids not observed. Lateral margins of proglottids quite straight, about the genital sinus a slight elevation or genital papilla.

Genital aperture marginal, irregularly alternating, situated a little anterior to the middle of the proglottid. Testes, numerous, 120-150, in medullary parenchyma between vitellaria. Vas deferens, a loose mass of coils between cirrus-pouch and middle of proglottid. Ductus ejaculatorius with few coils. Cirrus short and thick. Cirrus-pouch pear-shaped, 0.30 mm. long, extending about  $\frac{1}{3}$  across the proglottid breadth. Vagina, opening anterior to cirrus-pouch. Vaginal sphincter small, near opening. Lumen of first part of vagina broad, nearly as large as cirrus-pouch. No coils in vagina anterior to ovary. Arrangement of organs in interovarian space typical of genus. Ovary bilobed, posterior. Vitelline glands follicular, lateral, extending full length of segment. Uterus in ripe proglottid with many lateral outpocketings on either side. Eggs, round, thin shelled structures, size not given.

Habitat: Intestine of *Pimelodus pati* Valenc., Rio Paraguay, South America.

This species was described by Riggenbach (1896) who made it a member of the genus *Ichthyotaenia*. La Rue (1911) listed this species in a list of species of *Proteocephalus*. The material was collected by Dr. Ternetz in January and February 1894. The following description is based on Riggenbach's (1896) paper.

The worms as collected were of small size, 3.5-4.0 cms. long. There was no undamaged strobila. The neck is 0.85 mm. long and is quite broad. It passes imperceptibly into the youngest proglottids. The scolex (Fig. 133) is relatively large, and is perceptible to the naked eye. It bears four large suckers at its broadest zone. Here the scolex is 0.714 mm. broad. From this point the scolex becomes smaller toward the

end and also toward the neck. Its anterior region is conical. At the apex of the head is a slight depression which structurally is not a fifth sucker. There is no rostellum. The suckers are round in outline and they measure 0.34 mm. in diameter.

The youngest proglottids in the proliferation zone are narrow transverse bands 0.135 mm. long by 0.612 mm. broad. With increasing age the proglottids elongate until mature and ripe proglottids may be quadrate and the oldest proglottids even longer than broad. An end-proglottid was not seen. The margins of the segments are nearly straight. At the place of the opening of the genital passages the surface is slightly raised to form a small genital papilla.

In the head the excretory vessels run close together. Near the suckers a circular anastomosis unites the vessels. In the space between the suckers is a complicated plexus. The two pairs of main lateral excretory vessels run through the length of the worm in nearly a straight course. In the posterior margin of each proglottid is a transverse anastomosis connecting the main vessels. In this region also and in the neck short ducts arise from the main ventral vessels only and pass to the exterior, opening on the surface near the posterior angle of the proglottid. The lumen of such ducts becomes smaller near the periphery of the worm. The passage through the cuticula is quite small.

The genital aperture is marginal, irregularly alternating, situated a little anterior to the middle of the proglottid. A very small genital papilla is present, due largely to a thickening of the margin of the sinus. The anlagen of the genital organs appear in about the twentieth segment. The testes (Fig. 180) number 120-150 and are relatively small, 0.5 mm. in diameter, round or polygonal in outline. They fill the whole field between the two vitelline glands and the anterior and posterior margins of the proglottid. The vas deferens forms a loose mass of coils between the cirrus-pouch and the middle of the proglottid. The mass lies posteriad to the cirrus-pouch and is excentric to it, lying on the porose side of the proglottid. In the cirrus-pouch the ductus ejaculatorius forms a few coils and then it passes over into the cirrus. The cirrus is enlarged into a thick vesicle which fills up nearly the outer half of the cirrus-pouch. The cirrus-pouch, which is about 0.30 mm. long, reaches about  $\frac{1}{3}$  across the proglottid breadth. It is an elongated oval in shape.

The vagina which always opens anterior to the cirrus-pouch has a small sphincter near its opening. Further within, the lumen of the vagina enlarges into an ovoidal vesicle which may be almost as voluminous and as long as the cirrus-pouch. The vagina forms no coils anterior to the ovary. Riegenbach found no receptaculum seminis but he



found a widening of the vagina anterior to the ovary. The two dilations of the vagina take the place of the receptaculum seminis. The arrangement of the organs in the interovarial space is typical of the genus. The ovary is a bilobed structure, situated in the posterior part of the proglottid. The ovary does not seem to be made up of blind-pouches, as is true in the ovaries of most of the Taenias. Its outline is somewhat irregular, due to the sack-like processes which may be seen on the plump mass of the lobe. These extend posteriad nearly to the proglottid margin and laterally to the excretory vessels. The vitellaria as in all Proteocephalids are made up of a large number of single follicles arranged in long bands extending the full length of each lateral field of proglottid. The vitelline ducts arise in the posterior region of the segment and their course to the interovarial space is like that of other Proteocephalids. The shell-gland is poorly developed. The uterus lies in the middle of the proglottid and "As a canal with numerous lateral branches it extends itself through the whole proglottid." "The uterine eggs are round thin shelled structures." Their size was not given.

This species is readily separated from a large number of species of Proteocephalus on account of its lack of a fifth sucker. Among those species which do not possess fifth suckers this species is most like *P. sulcatus* which likewise occurs in one of the Siluridae. The latter species however is much larger as to head and as to observed length. It also has a much larger number of testes. The form of the head is also different.

#### PROTEOCEPHALUS SKORIKOWI (Von Linstow)

[Figs. 152, 177]

1904: <i>Ichthyotaenia skorikowi</i>	von Linstow	1904:18-19
1911: <i>Proteocephalus skorikowi</i>	La Rue	1911:475

This species was described by von Linstow (1904). La Rue (1911) listed it among other species of Proteocephalus. The following description is an abstract from von Linstow's account.

The length measures as much as 200 mm., the breadth anteriorly 1.14 mm. First proglottids beginning directly behind the scolex are very short. Breadth in middle is 3.75 mm; the length of proglottids here 0.95 mm. Breadth at posterior end equals 3.16 mm; length of proglottids here 1.97 mm. The last proglottid is rounded posteriorly. The scolex is short, 0.67 mm. broad. Von Linstow's drawing of the head is reproduced (Fig. 152). Suckers measure 0.250 mm. in diameter

while a fifth apical sucker is 0.130 mm. in diameter. Muscles of subcuticular layer are as usual. The heavy layer of longitudinal muscles below the subcuticula in the anterior part of the worm is very strongly developed, filling up almost the entire space in unripe proglottids. Dorsoventral muscles are very heavily developed. In anterior segments the main longitudinal nerves lie about  $12/100$ , and in ripe segments about  $6/100$ , of the segment width from the lateral margins. Mesad of the nerve trunks lie the excretory ducts two on either side. Chalkbodies are lacking entirely.

Sexual openings are marginal, irregularly alternating, posterior to the middle in each proglottid. The vagina lies anterior to the cirrus. The cirrus is cone-shaped, blunt at the tip, 0.141 mm. long. The point is 0.042 mm. broad. The cirrus-sheath extends  $1/5$ - $1/6$  across the breadth of the proglottid. The vas deferens makes many coils before entering the cirrus-sheath. Testes are very numerous, 0.053-0.083 mm. in diameter. From von Linstow's figure one may conclude that there are about 70-100 testes. The vagina runs in a curve to the middle of the posterior region of the segment where it forms many coils anterior to the ovaries. These coils function as a receptaculum seminis. The ovary is made up of two groups of club-shaped bags which run parallel to the posterior margin of the proglottid. Anterior to its middle lies an oöcapt. Vitellaria are follicular, reaching on left and right the full length of the proglottid inside the longitudinal muscles. The uterus in the posterior part fills the whole space within the longitudinal muscle fibers and extends anteriorly in round diverticula. In von Linstow's drawing which is reproduced (Fig. 177) there are 6-8 diverticula on either side. Eggs are globular, 0.027 mm. They have two membranes, the outer one very delicate and hyaline. The six-hooked embryo measures 0.021-0.023 mm. in diameter.

Habitat: Intestine of *Acipenser stellatus* (type host); River Gürgen, Caspian Sea (type locality). Von Linstow failed to state who collected the specimens of this species and the abundance of their occurrence.

This species is one of the more robust Proteocephalids and is thus distinguished from a large number of species of the genus. The fact that the vagina forms many coils anterior to the ovary and that the ovary consists of slender club-shaped bags separates it effectively from all other known species. The position of the genital pore posterior to the middle of the proglottid is a further distinguishing feature. In many respects this species most closely resembles *P. fossatus* (Riggenbach).

## PROTEOCEPHALUS SAGITTUS (Grimm)

(?)1819:	<i>Bothriocephalus barbatulae</i>	Rudolphi	1819:144
(?)1850:	<i>Bothriocephalus barbatulae</i>	Diesing	1850:608
1872:	<i>Taenia sagitta</i>	Grimm	1872:240-243
1878:	<i>Taenia sagittata</i>	von Linstow	1878:260
1891:	<i>Taenia sagittata</i>	Monticelli	1891:169
1896:	<i>Ichthyotaenia sagittata</i>	Riggenbach	1896:267
1909:	<i>Ichthyotaenia sagitta</i>	Lühe	1909:33
1911:	<i>Proteocephalus sagittus</i>	La Rue	1911:475

Specific Diagnosis: Strobila small, as much as 45 mm. long by 1 mm. broad. Head thick, ending in an unarmed point. Suckers four, in pairs on the basal part of the head. Suckers transversely elongated and heavily muscled. Neck as much as 12 mm. long by 0.5 mm. broad. (Probably many young proglottids were overlooked in this exceptionally long neck.) Proglottids few. Youngest proglottids about quadrate, older ones longer. Last eight proglottids 1.4-1.5 mm. long by 1 mm. broad by 0.3 mm. thick. Last proglottid always rounded posteriorly. Cirrus-pouch large and clubshaped. Cirrus quite thick. Uterus with uterine pouches, number unknown. Genital pore situated near middle of lateral margin of proglottid.

Habitat: In intestine of *Cobitis barbatula* (type host), Petersburg (type locality) and Province of Novgorod.

Grimm (1872:240-243) described some cestodes which he had collected from the intestines of *Cobitis barbatula* at Petersburg and in the province of Novgorod. These he named *Taenia sagitta*. He called attention to the fact that Rudolphi (1819:144) had proposed the name *Bothriocephalus barbatulae* for some cestodes from *Cobitis barbatula*. Rudolphi gave no diagnosis nor description hence it is not possible to determine the genus to which his specimens belonged. Grimm also called attention to Diesing's (1850:608) reference to *Bothriocephalus barbatulae* and that Diesing gave no description of the form. Von Linstow (1878:260) listed *Taenia sagittata* Grimm (for *sagitta*) as a parasite of *Cobitis barbatula*. Monticelli (1891:169) included *Taenia sagittata* (for *sagitta*) in a list of cestode species parasitic in fish. Riggenbach (1896:267) included *Ichthyotaenia sagittata* (Grimm) in a list of *Ichthyotaenia*. Lühe (1909:33) gave a very short diagnosis of *Ichthyotaenia sagitta* (Grimm) which he apparently derived from Grimm's (1872) paper. La Rue (1911:475) included this species in a list of *Proteocephalus* species.



Because of its inaccessibility to many scientific workers Grimm's entire description of this species is here quoted, and since the tables at the end of this section give the essential data no digest of his paper is given at the end of his description:

"TAENIA SAGITTA.—Der berühmte Helmintholog Rudolphi erwähnt in seinem Werk Entozoorum Synopsis S. 144 eines Bandwurmes, den er im Darne von *Cobitis barbatula* aufgefunden hat. Da er aber nur ein Fragment, nicht aber ein volles Exemplar des Wurmes besass, so gab er auch keine eingehendere Beschreibung dieser als neu von ihm erkannten Art, sondern stellte sie grade zu den Grubenköpfen und belegte sie mit dem Namen *Bothriocephalus barbatulae*. Diesing stellte diese Art in seinem *Systema helminthum* zu den *Species dubiae* und setzte zu den von Rudolphi gesagten nur noch hinzu, dass "Fragmenta acephala servantur im M. C. V." (*Syst. helm.* I. p. 608). Etwas umständlicher spricht sich S. Leuckart aus über das Aussehen dieses Helminthen, indem er sagt, "an dem sehr kleinen kopflosen Stücke, das ich sah, war nichts Ausgezeichnetes. Die Glieder länger als breit, oder vollkommen quadratisch. Keine deutlichen Ovarien" (*Sig. Leuckart, Zoologische Bruchstücke.* I. p. 57). Das ist Alles, was wir von diesem Bandwurme kennen und deshalb wird wohl nicht überflüssig sein, wenn ich im folgenden die Resultate meiner anatomischen Untersuchung kurz zusammen fassen werde, die ich an diesem Wurm unlängst angestellt habe.

"Ich fand nämlich hier, in Petersburg, und im Nowgorod'schen Gouvernement 3 erwachsene Exemplare des Wurms in *Cobitis barbatula*, nachdem ich einige Hunderte dieses so häufig in unseren kleineren Flüssen vorkommenden Fischchens durchmustert hatte. Aus dem Gesagten geht schon hervor, dass dies ein sehr seltner Wurm sein muss. Hier muss ich noch bemerken, dass, dem Kopfe nach, dieser Wurm der *Taenia filicollis* Rud. nicht unähnlich ist, sich aber von ihr durch die längeren Glieder, wie wir es unten sehen werden, unterscheidet.

"Die Länge des grössten Exemplares betrug 45 Mm. bei einer Breite von 1 Mm. Der Kopf ist verdickt und endigt mit einer Spitze die keine Hacken trägt; die 4 Saugnäpfe liegen paarweise auf der Grundhälfte des Kopfes; sie sind etwas in die Quere verlängert und stark muskulos, weshalb der Wurm auch so fest an die Wände des Darms sich ansaugt, dass man beim Einsammeln sehr vorsichtig sein muss, wenn man nicht "Fragmenta acephala" erhalten will. Das zu seiner Basis verengte Kopfchen geht in den ziemlich dünnen Hals über, welcher ungefähr 12 Mm. lang und 0,5 Mm. breit ist. Hinter dem Halse fängt die Kette an, in der ich 23 einzelne Glieder gezählt habe. Die ersten resp. jüngsten Glieder sind fast vollkommen quadratisch; weiterhin werden sie etwas länger, so dass die letzten acht Glieder 1,4 bis 1,5 Mm. lang sind; dabei beträgt ihre Breite 1 Mm., bei einer Dicke von nur 1,3 Mm., so dass der Wurm vollkommen plattgedrückt erscheint. Das letzte Glied ist immer von hinten abgerundet. Dies ist alles was wir an einem unlädirten Exemplare zu sehen bekamen.

"Wenn wir nun aber einzelne zuvor mit Carmin und Glycerin bearbeitete Glieder und dünne Querschnitte unter dem Mikroskop untersuchen, so überzeugen wir uns, dass der Bau der Körpermasse dieses Bandwurmes sich überhaupt durch

nichts von dem Bau anderer Bandwürmer unterscheidet. Wir finden hier wie auch bei *Cyathocephalus truncatus*, dass der Körper aus folgenden Elementen besteht:—aus der körnchenreichen Grundsubstanz, die von sich schlängelnden dorso-ventralen Muskelbündeln durchsetzt wird; einer Schicht Längen-muskeln und einer Schicht Quer—oder Ringmuskeln, einer Schicht feinkörniger Rinden-substanz, in der die Enden der dorso-ventralen Muskeln liegen, und endlich der sehr feiner äusseren Haut, die gar keine Muskeln besitzt. In der Längsaxe eines jeden reifen Gliedes liegt das centrale Rohr des Eierstocks, welcher aber manchmal näher zur einen oder andern flachen Seite zu liegen kommt, wie man es auf den Querschnitten bemerkt. Von diesem Centralrohr verlaufen nach beiden Seiten zu unregelmässig gebogene und theils sich auch verzweigende Ausläufer, die in ihrer Länge mittelst der dorso-ventralen Muskeln erhalten werden. In der Mitte des Hauptrohres geht von ihm die Scheide ab, die, nachdem sie eine schwache Biegung gemacht hat, sich in der Mitte der seitlichen Oberfläche des Gliedes nach aussen öffnet; die Scheide ist ziemlich breit, so dass die Eier sie leicht passiren können. In dem von mir untersuchten Exemplare waren die Eier in der Mehrzahl der Glieder vollkommen reif;—sie enthielten eine grob und—feinkörnige Masse und waren mit einer ziemlich dicken Haut umgeben. Aber wie in diesen reifen Gliedern, so auch in den jüngern bin ich nicht im Stande gewesen die sog. Dotterstöcke aufzufinden; ob sie hier so früh verschwinden, oder zu fein sind, weiss ich nicht; auf den Querschnitten sind sie aber nicht aufzufinden.

“Gleich über der Scheide liegt und öffnet sich nach aussen das männliche Zeugungsorgan; dasselbe besteht aus einem ziemlich grossen und kolbenförmigen Cirrusbeutel, in dem der eingezogene Cirrus liegt; der Cirrus ist ziemlich dick und am Grunde dünner als am Ende; dessen Kanal ist durch den Cirrusbeutel zu sehen. In den Wänden des Cirrusbeutels trafen wir, wie immer, Längs—und Quermuskeln. Die Samendrüsen waren nicht zu sehen.

“Dies ist alles was ich von dem Bau des Bandwurmes erfahren konnte. Die Unvollkommenheit meiner Untersuchung wurde aber durch den Mangel an Material bedingt. Dennoch aber fühle ich mich berechtigt zu sagen, dass auch dies Wenige genügt, um dem beschriebenen Bandwurm seine natürliche Stellung in der Reihe seines Gleichen anzuweisen und somit die Zahl der zweifelhaften Arten zu beschränken.

“Noch muss ich hinzusetzen, dass aus dem Gesagten doch klar ist, dass ich wohl mich nicht irre, indem ich den von mir aufgefundenen Wurm als dem *Bothriocephalus barbatulae* Rud. identisch halte.”

While the foregoing description is sufficient to warrant the inclusion of this species in the genus *Proteocephalus* it is not sufficient to enable one to determine the relations of the species to the other members of the genus. In size the form resembles *P. filicollis* and *P. agonis*. For the present the species must be put in the list of incompletely described species.

## PROTEOCEPHALUS SALVELINI (Linton)

[Figs. 143, 144]

1897: <i>Taenia salvelini</i>	Linton	1897:424
1911: <i>Proteocephalus salvelini</i>	La Rue	1911:475

Linton (1897:424) described this species. La Rue (1911:475) included this form in a list of species of *Proteocephalus*.

Linton's description reads:

"TAENIA SALVELINI. *Type*.—No. 4811, U. S. N. M. From intestine of Great Lake trout (*Cristivomer namaycush*); Outer Island, Lake Superior; J. W. Milner. In this lot are several small *Taeniae*; scolices with few roundish or oblong segments, in some of which the male genitalia were developed, otherwise immature; length from 3 to 5 mm.

"These specimens bear some resemblance to the young of *T. torulosa*, Batsch, as described by Zschokke (1884).

"Head usually rounded in front, with suckers directed anteriorly. The diameter of the head varies according to state of contraction, usually 0.3 to 0.4 mm.; suckers relatively large, usually directed forward, prominent, rather deep. 0.15 to 0.18 mm. in diameter, aperture 0.1 mm. in diameter. Neck assuming various contraction shapes; in some continuous with head and merging imperceptibly in body; in others separated by a constriction behind the head; in others not separated from head by constriction but with segments beginning abruptly; numerous calcareous bodies in neck behind head. Usually first segments indistinct, broader than long. Oldest segments longer than broad; genital aperture near middle of lateral margin a little nearer anterior margin. Vitellaria making a narrow border along lateral margins; beginning of germ gland at posterior end; central region in front of rudimentary germ gland occupied by prominent testicular lobes; cirrus-bulb oblong, elliptical, convex on posterior, straight or slightly concave on anterior surface; cirrus enters from inner anterior edge of bulb, then traverses middle of bulb to orifice; length of bulb, 0.26 mm.; diameter, 0.14 mm.; largest segments, 1.5 mm. in length and 0.75 mm. in breadth."

Linton's figures of the head are reproduced (Figs. 143, 144).

Since this description is insufficient for determination in comparison with the forms described here Dr. H. B. Ward very kindly secured Linton's specimens from the National Museum at Washington. Unfortunately but fragments remained. These fragments were cleared and examined in glycerine. The writer's observations on the heads agree very well with Linton's records. A fifth sucker or a trace of one could not be found. The suckers in their maximum diameter measure 0.170 mm. the sucker opening about 0.100 mm. The head is flattened dorso-ventrally. In general shape it resembles some dilated heads of *P. pinguis* but is larger. Linton says that it resembles young specimens of *P. torulosus*, however its measurements are quite different. It must be left for the present in the list of inadequately described species.



## PROTEOCEPHALUS CYCLOPS (Von Linstow) sp. inq.

[Fig. 159]

1877: *Taenia cyclops* von Linstow, 1877:15-16.

Von Linstow's description of this immature form is here given:

"*Taenia cyclops* n. sp.—In *Coregonus maraena* aus dem Schallsee. Die Tänie ist 25 Mm. lang und 0,27 Mm. breit, überall fast gleich breit, die letzte Proglottide hinten zugespitzt. Die Kalkkörperchen sind klein, ohne concentrische Schichtung; das Kopfende ist abgerundet, die Saugnäpfe sind längsoval, 0,15 Mm. lang und nach hinten zugespitzt, 0,1 Mm. breit; ein fünfter scheitelständiger Saugnäpf hat 0,069 Mm. im Durchmesser; Geschlechtsorgane waren noch nicht vorhanden. *Taenia longicollis* aus verschiedenen zur Familie der Lachse gehörenden Fischen hat zum Unterschied von dieser Art länglichrunde Saugnäpfe, deren längerer Durchmesser rechtwinklig zur Längsaxe des Thieres steht."

Nufer (1905:152) thought that this form was a larval state of *P. longicollis* (Rud.). However, the character of the suckers does not permit such a determination. *P. cyclops* is remarkable for the notch in the inferior margin of the sucker and in this respect differs from all the other species of *Proteocephalus*. This notch is well shown in von Linstow's drawing which is reproduced (Fig. 159). Until adults can be secured for determination this form must be considered to be a species inquirenda.

## PROTEOCEPHALUS HEMISPHERICUS (Molin) sp. inq.

1859:	<i>Taenia hemispherica</i>	Molin	1859:14
1896:	<i>Ichthyotaenia hemisphaerica</i>	Riggenbach	1896:267, 268
1911:	<i>Proteocephalus hemisphericus</i>	La Rue	1911:475

Molin's original description and observations are as follows:

"*Taenia hemispherica* Molin.—*Caput hemisphericum, acetabulis anticis; ore inermi; collum longissimum, antice dilatatum; articuli supremi brevissimi, subse-quentes transverse parallelogrammici, postremi subquadrati; aperturæ genitales marginales, vage alternæ. Longit. 0.07; lat. 0.003.*

"HABITACULUM. *Anguilla vulgaris*: in intestino tenui, Novembri, Patavii (Molin).

"OSSERVAZIONE 1. Ai 5 di Novembre del 1858 rinvenni nell' intestino di un' anguilla, nella quale avevo trovato 5 *Dibothrium claviceps*, un esemplare di quel verme; ed in un' altra anguilla un esemplare intero e vari frammenti.

"OSSERVAZIONE 2. Negli articoli bene sviluppati potei distinguere ai margini laterali le uova, e tutto il resto dell' articolo riempito dall' amplissimo

ovidotto ravvolto in ambagi e ripieno di uova sferiche. Nel mezzo vidi collocato orizzontalmente il membro virile attortigliato che si estendeva fino al centro dell' articolo.

"OSSERVAZIONE 3. Fino ad ora non si conosceva dell' anguilla altro che la *Taenia macrocephala*, dalla quale però la *hemisphaerica* si distingue per la forma della testa non chè per la lunghezza del collo. Questa è affine alla *filicollis*, dalla quale però si distingue per la forma della testa e del collo, e deve perciò venir registrata dopo di questa nel sistema."

Since the appearance of Molin's paper no further attempts have been made to describe this species. There is in fact no further notice of the finding of this species. Linton (1886) thought that his *Taenia dilatata* might be the same as *Taenia hemispherica*. Riggenbach (1896) said of it, "Ein genauer Vergleich der Diagnosen, welche die genannten Autoren den fraglichen Species gaben, zwingt mich mit Bestimmtheit eine Identität der *I. (Ichthyotaenia) dilatata* Linton mit *I. hemispherica* Molin anzunehmen." Linton's species has been determined by the writer to be identical with *Proteocephalus macrocephalus* (Creplin). Schneider (1903) identified a cestode taken from *Anguilla vulgaris* as *Ichthyotaenia hemispherica*. Later (1905) he decided that this form was not *I. hemispherica* but *I. macrocephala* (Creplin). His statement of this is discussed in the historical summary of *Proteocephalus macrocephalus*. Nufer (1905) attempted to show the identity of *P. dilatatus* (Linton) and *P. hemisphaericus* (Molin) and further that these species were identical with *P. macrocephalus* (Creplin). This contention is true in part at least. In the discussion of *P. macrocephalus* in another part of this monograph identity of *P. dilatatus* and *P. macrocephalus* has been shown. The present form, however, is so little known and so poorly described that it seems advisable for the present to consider that it is not identical with the well known species of *Proteocephalus* found in *Anguilla* but that it is a species inquirenda. La Rue (1911:475) listed this form among other species of *Proteocephalus*.

## PROTEOCEPHALUS MACROPHALLUS (Diesing) sp. inq.

1850:	<i>Taenia macrophalla</i>	Diesing	1850:514
1856:	<i>Taenia macrophalla</i>	Diesing	1856:35
1864:	<i>Taenia macrophalla</i>	Diesing	1864:377
1891:	<i>Taenia macrophalla</i>	Monticelli	1891
1896:	<i>Ichthyotaenia macrophalla</i>	Riggenbach	1896:267

This form is known only from the writings of Diesing listed above. His statements are wholly inadequate for purposes of comparison and his drawings (Diesing 1856, Pl. VI, figs. 15-20) show but little more than external features and the cirrus pouch. It seems to the writer however that this species should be considered as belonging to the genus *Proteocephalus* and that it is a species inquirenda. Monticelli (1891) and Riggenbach (1896) included this species in their groups of fish cestodes the most of which are now included in the genus *Proteocephalus*.

Diesing's original species description (Diesing 1850:514) is here quoted: "*Taenia macrophalla* Diesing. *Caput* rotundatum depressum, acetabulis anticis maximis. *Collum* nullum. *Articuli* supremi, subquadrati, subsequi oblonge-quadrati, ultimo longissimo rotundato. *Aper-turae* genitalium marginales. *Penes* alterni longissimi filiformes. Long. 1-3'"; latit.  $1\frac{1}{2}$ '".

"*Habitaeculum*. *Cichla monoculus*, Junio, Julio et Octobri in Brasilia (Natterer: in intestinis. M. C. V.)

"b. Os limbo elevato, uncinulorum corona interdum decidua armatum."

## PROTEOCEPHALUS NEMATOSOMA (Leidy) sp. inq.

1888:	<i>Taenia leptosoma</i>	Leidy	1888:169, (nec Diesing)
1891:	<i>Taenia nematosoma</i>	Leidy	1891:410-418
1891:	<i>Taenia somatolepta</i>	Monticelli	1891
1911:	<i>Proteocephalus nematosoma</i>	La Rue	1911:475

In May 1888 Leidy reported thus on the "Parasites of the Pickerel".

"Dr. Leidy remarked that among the numerous parasites which are mentioned as infesting the pike, *Esox lucius*, of Europe, no *Taenia* is indicated. In the Pickerel, *Esox reticulatus*, brought to our market, a species of the latter appears to be common. In two fishes he found half a dozen in the intestine and stomach; and in another a single individual two feet in length. It resembles



closely the *Taenia ambloplitis*, noticed in the Rock Bass, *Ambloplites rupestris* (Proc., 1887, 23), and may be the same. Distinguishing it with the name of *Taenia leptosoma*, its characters are as follows: Body long and thin, and at the forepart thread-like. Head unarmed, without rostellum, with four equidistant hemispherical bothria; neck very short or none; anterior segments transversely linear, many times wider than long; posterior segments gradually becoming proportionately longer and quadrate and barrel shaped; genital apertures marginal, alternating irregularly. Ova spherical.

"Length from 6 to 9 and 26 inches, shortening to one half or less; breadth to 2 and 2.5 mm. Head 0.25 to 0.5 mm. broad; bothria 0.125 to 0.175 mm. Anterior segments an inch from the head 0.175 mm. long by 1 mm. broad; posterior segments 0.5 to 0.75 mm. long by 2 to 2.5 mm. broad. Ova 0.028 to 0.032 mm. in diameter.

"A single slender *Scolex* associated with the longest *Taenia* was 4 mm. long by 0.25 wide, but elongated to 8 mm. by 0.1 wide. The head was of the same form as that of the *Taenia*. After being in alcohol, the head of the *Scolex* was 0.225 mm. wide, with the bothria 0.1 in diameter. The posterior part of the body exhibited traces of segmentation, with the segments 0.075 mm. long by 0.25 wide."

In November 1890 from the same host species Leidy reported *Taenia nematosoma*. His description is quoted:

"*Taenia nematosoma*, n. s.—Head rounded quadrate, unarmed, with equidistant hemispherical bothria and a small central papilla; neck short or none; fore part of body linear; anterior segments much wider than long; posterior segments gradually becoming proportionately longer, quadrate or barrel-shaped; genital apertures marginal and alternating irregularly. Length to 9 inches, contracting to about one-half. Breadth of head 0.375 to 0.5 mm.; bothria 0.175 wide; neck 0.25 wide; anterior segment an inch from the head 0.175 mm. long by 2 mm. broad; posterior segments 0.75 mm. long by 2 mm. broad, and when contracted widening to 2.5 mm. Ova spherical, 0.028 to 0.032 mm.

"A half dozen specimens in the stomach of two Pickerel, *Esox reticulatus*."

Neither report was accompanied by drawings.

Leidy's two forms agree in practically every particular as to measurements and proportions and host species. The writer therefore concludes that they are identical and includes them both under the name *P. nematosoma* (Leidy). This species differs from *P. ambloplitis* chiefly in the measurement of the suckers. Its measurements vary greatly from those of *P. pinguis* and from *P. esocis* Schneider. None of Leidy's specimens remain, so the species must continue a species inquirenda. Monticelli (1891) on account of the confusion of this name with *Taenia leptosoma* Diesing suggested the name *Taenia somatolepta*. However the name *nematosoma* should be preferred because it is an earlier available name than *somatolepta*. La Rue (1911:475) made this one of his list of *Proteocephalus* species.

## PROTEOCEPHALUS SALMONIS-UMBLAE (Monticelli) sp. inq.

(?)1811-12:	<i>Taenia salmonis omul</i>	Pallas	1811-12:409
1884:	<i>Taenia salmonis umblae</i>	Zschokke	1884:18-19
1891:	<i>Tetracotylus salmonis-umblae</i>	Monticelli	1891:
(?)1891:	<i>Tetracotylus salmonis-omul</i>	Monticelli	1891:
1896:	<i>Ichthyotaenia salmonis-umblae</i>	Riggenbach	1896:267
1896:	<i>Ichthyotaenia salmonis umblae</i>	Zschokke	1896:783
1909:	<i>Ichthyotaenia salmonis umblae</i>	Lühe	1909:33
1911:	<i>Proteocephalus salmonis-umblae</i>	La Rue	1911:475

This species was first described and delineated by Zschokke (1884) who found it in *Salmo umbla*, Lake Geneva. His description and drawings are inadequate for a determination of its position. Monticelli (1891) considered this to be a species of *Tetracotylus*. He also stated that he considered *Taenia salmonis-omul* Pallas a species dubia and probably a synonym of *T. salmonis-umblae*. Monticelli wrote both of these names with a hyphen and hence was the first to give these species binary names. Krämer (1892) does not discuss the species. Riggenbach (1896) considered it to be a species of *Ichthyotaenia*. He did not add anything to our knowledge of its structure.

Zschokke (1896:783) listed this species in his summary of parasites found in the fishes of Lake Geneva. He did not find it in any of the fish from the Rhine altho he examined nearly 1200 fish. Nufer (1905) who investigated the fish of Lake Lucerne made no report on this species. Lühe (1909) placed this species in the genus *Ichthyotaenia*. Since his diagnosis is short and concise it is here quoted in lieu of Zschokke's description (1884:18-19):

“*Ichthyotaenia salmonis umblae* Zschokke. 30-50 cm. lang, 1-2 mm. breit. Am Scheitel eine leichte saugnäpfähnliche Vertiefung. Proglottiden länger als breit, ca. 100 bis 150 an Zahl, Hodenbläschen zahlreich; ein hodenfreies Mittelfeld scheint zu fehlen. Cirrus-beutel bis fast zur Mittellinie reichend; Genitalöffnung ungefähr an der Grenze von 2. und 3. Fünftel der Proglottidenlängs. Uterus mit “zahlreichen” (ca. 6 ?) Blindsäcken jederseits. Kalkkörperchen sehr zahlreich, besonders in Scolex und Hals.

“Im Darm von *Salmo salvelinus* L.; bisher nur aus dem Genfer See bekannt.”

This species is too little known to permit a determination of its position in the genus. On account of its larger size and more numerous testes it seems certain that it is not the same as *P. fallax* or *P. dubius*. It does somewhat resemble the *P. neglectus* from *Trutta fario* and there

is a possibility that it may be the same. For the present it must be considered to be a species inquirenda. In regard to the name of this species attention is called to the fact that Zschokke wrote the name as a trinomial. Since a trinomial name can have no standing and since Monticelli (1891) first wrote this name as a binomial it is here suggested that the name should be credited to him. The species is then to be known as *Proteocephalus salmonis-umblae* (Monticelli). Pallas (1811-12) is inaccessible to the writer. It appears that his description of *Taenia salmonis omul* if one were given was of no value. Monticelli (1891) suggested that *Taenia salmonis-umblae* was probably identical with the *Taenia salmonis-omul* Pallas and he called the latter a species dubia. Rudolphi (1819:175) expressed the opinion that *Taenia salmonis omul* was a species of *Bothriocephalus*. For this reason it seems that *Taenia salmonis omul* is hardly of sufficient value as a name to be worthy of being called a species inquirenda and since Monticelli apparently desired to bury it with the *Taenia salmonis-umblae* it is best not to attempt to resurrect it. La Rue (1911:475) in a list of *Proteocephalus* species credited this species to Monticelli who was the first to give it a binary name.

PROTEOCEPHALUS OSCULATUS (Goeze), sp. inq.

[Figs. 161-165, 182]

1782:	<i>Taenia osculata</i>	Goeze	1782:415
1782:	<i>Taenia alternatim transverse lineata</i>	Goeze	1782:416
1786:	<i>Taenia siluri</i>	Batsch	1786:157-159
1786:	<i>Taenia osculata</i>	Batsch	1786:209
1788:	<i>Taenia osculata</i>	Schrank	1788:47
1788:	<i>Taenia glanis</i>	Schrank	1788:47
1790:	<i>Taenia percae</i> $\beta$	Gmelin	1790:3079
1790:	<i>Taenia siluri</i>	Gmelin	1790:3080
1803:	<i>Halysis siluri</i>	Zeder	1803:353
1803:	<i>Halysis transverse-lineata</i>	Zeder	1803:353
1810:	<i>Taenia calycina</i>	Rudolphi	1810:115-116
1810:	<i>Taenia osculata</i>	Rudolphi	1810:116-119
1819:	<i>Taenia osculata</i>	Rudolphi	1819:150, 497
1845:	<i>Taenia osculata</i>	Dujardin	1845:584
1850:	<i>Taenia osculata</i>	Diesing	1850:522-523
1854:	<i>Taenia osculata</i>	Wagener	1854
1861:	<i>Taenia osculata</i>	Van Beneden	1861:165
1896:	<i>Ichthyotaenia osculata</i>	Riggenbach	1896:267
1909:	<i>Ichthyotaenia osculata</i>	Lühe	1909:30-31
1911:	<i>Proteocephalus osculatus</i>	La Rue	1911:475



Specific Diagnosis: For the specific diagnosis see Lühe's diagnosis of this species at the close of the historical summary.

Habitat: In intestine of *Silurus glanis* L.

Host	Locality	Collector	Authority
<i>Silurus glanis</i> L.	Magdeburg	Goeze	Goeze 1782:415-416
<i>Silurus glanis</i> L.	Greifswald	Rudolphi	Rudolphi 1819:150

Goeze (1782:415) described and figured this form from the intestine of *Silurus glanis*. His diagnosis is here given:

"Der gemündete Bandwurm. *Taenia osculata*. Auch vom Graf von Borke in den Gedärmen eines 24 pfündigen Welses (*Silurus Glanis* L.). Nach der Grösse dieses Fisches wenige, und äusserst kleine Tänien. Kleiner, als in der Hechten. Nicht am Magenende, sondern mehr in der Gegend des Afters. Das merkwürdigste daran, das sie ausser den beyden Saugblasen am Kopfe, an dem vorstehendem Rüssel eine wahre Mündung hatten, welche unter dem Komposito mit No. 4 Tub. B. deutlich zu sehen war. An keinem andern hat der Graf die Rüsselmündung so deutlich, als an diesen wahrgenommen. Sie waren alle lebendig; aber auf der Glasplatte schwer zu behandeln, weil sie sich beständig krümmten, und mit ihren Saugwarzen selbst an ihrem eignen Körper vest ansogen. Ein besondere Umstand! Das Aufblähen der Saugwarzen, und das Ausstrecken und Einziehen des Rüssels ein angenehmes Schauspiel. Die Glieder sehr undeutlich. Mehr Runzeln als Glieder."

Goeze (1782:416) described a form from *Silurus glanis* which he thought was a species distinct from the *Taenia osculata*. Later investigators considered that the second form was identical with *Taenia osculata* and it seems that they are probably correct. Goeze's description of the second form is more complete than that of the first hence it is here quoted:

"Der wechselsweise Lineirte Bandwurm. *Taenia, alternatim transverse lineata*: articulis *quadrangularibus*; capite quadri verrucoso.

"Eine wirklich neue und besondere Art. Auch aus den Gedärmen eines sechzehn pfündigen Welses (*Silurus Glanis*, L.) Als ich am 1sten Julius 1780 von Rekane nach Magdeburg kam, blieb ich daselbst um der grösseren Fische willen nach einige Tage. Ich bekam die Gedärme eines Störs (*Acipenser Sturio* L.) von 50 Pfund. In denselben verschiedene Askariden, und zween Kratzer, wie bey andern Fischen. In den Gedärmen eines Welses aber fand ich zween merkwürdige Bandwürmer.

"Die Länge etwa 12 Zoll. Die Breite am breitestem Hinterende eine gute Linie. Die Glieder regelmässige Quadrate: eine Linie lang und Breit. Nach dem Kopfe zu Verhältnissmässig kleiner. Das Charakteristische dieses Wurms waren

die, Wechselsweise, in jedem Gliede, in ungleicher Ordnung stehende weisse Querlinien, die bis über die Hälfte des Körpers, vom Hinterende an, hinaufgehen, und besonders in die Augen fallen. Diese Linien gehen nicht weiter bis in die Mitte des Gliedes. Zeigt sich z. B. auf der rechten Seite in jedem Gliede, in fünf nach einander, die weisse Querlinie; so ist die linke Seite frey. Dann auf der linken Seite in zwey Gliedern, und die rechte Seite frey. Weiter nur an einem Gliede, bald rechts, bald links, u. s. w. In der Mitte jedes Gliedes am Hinterende liegen reife Eyer, und ich kann diese Linien für nichts anders, als für Eyergänge halten, obgleich die Randmündungen zu klein, oder zu verschlossen sind, als dass man sie wahrnehmen könnte. Das Kopfe sehr fein und dünne, aber flach, und das Köpfchen nach Proportion wie ein kleines Knötgen. Unter dem Komposito der Hals ungegliedert. Am Kopfe auf jeder Seite zwey stark hervorstehende Saugmündungen. Vorn ein kurzes Rüsselchen, ohne Baken."

The "Querlinien" of the above description is probably the more or less clear region in which the cirrus-pouch, vagina, and the convoluted vas deferens lie.

Goeze's figures of this form have been reproduced (Figs. 163, 164, 165).

Batsch (1786) followed Goeze in considering that two species of *Taenia* were parasitic in *Silurus glanis*. He changed the name of Goeze's second form to *Taenia siluri*. His two descriptions which seem to be based largely on the work of Goeze are here quoted:

"*Taenia siluri*. Der Welsbandwurm.

"Goetze, S. 416. T. 33. fig. 11-14. *Taenia* (scalaris) ductu rectissimo brevi introrsum subclavato, extrorsum pedicellato; capite papillis quatuor et nodo verticali subaequalibus globosis; articulis subquadratis, marginibus convexis.

"In jedem reifen Gliede hat der Eiergang, fast wie bei dem vorigen, die Gestalt eines Stempels, in dem er mit dem Eierstocke, welcher in der Mitte des Gliedes liegt und eiförmig ist, zusammenfliesst. Aber der Gang ist kürzer, gerader, und der Eierstock weder hervorragend noch so ausgebreitet und deutlich von dem Eiergange an Grösse verschieden.

"Die Glieder sind viereckig, eine Linie lang und breit, und an den Ecken abgerundet, und an den Seiten mit einem ziemlich breiten dunkeln Rande.

"Die Eierstöcke und Gänge sind von weisser Farbe, und stehen wechselsweise auf einer oder der andern Seite, in verschiedner Anzahl neben einander, wie bei den vorigen Art. Sie sind vom Hinterende bis über die Hälfte des Körpers sichtbar, wo die Glieder aufhören viereckig zu sein, sondern ganz kurz werden, und auch von da an mit dem ganzen Vorderende des Körpers gleichförmig bis an den Kopf an Breite abnehmen. Nahe am Kopfe hat der Körper etwa den sechsten Theil der Breite der reifen Hinterhälfte. Das Vorderende ist flach.

"Der Hals ist lang und ungegliedert; der Kopf ragt wie ein starker Knoten hervor, der aus vier kuglichen grossen nahe beisammen stehenden Saugblasen, und einem beinahe eben so grossen Knöpfchen auf dem Scheitel zusammengefasst ist.

“Jede Saugblase hat einem breiten wulstigen Rand um ihre tiefe Höhle; und giebt dem Kopfe eine ausgezeichnete Schönheit.

“Die Länge des ganzen Körpers erstreckt sich auf zwölf Zoll. Diese Art wohnt in den Gedärmen des Welses (*Silurus Glanis*), Goetz hat zwei Zeichnungen davon gegeben, deren eine darin von dem beschriebnen abweicht, dass die Hinterglieder zwar viereckig sind, aber doch mit dem etwas breitem Hinterrande über den folgenden Vorderrand eckig hervorstehen, und keine Eiergänge zeigen. Der Kopf ist übrigens in der Hauptsache nicht verschieden.

“Die Oeffnungen der Eiergänge und die Art der Eier selbst ist an dieser Art noch nicht berichtet.”

“*Taenia osculata*. Der gemündete Bandwurm.

“Götze S. 415, T. 33. fig. 9. 10.

*Taenia* (larvata) capite cum collo coalito, oculis binis speciosis bimarginatis, in acumen osculatum defluente; corpore crenato, articulis brevibus, parallelepipedis.

“Dieser Bandwurm, den der Graf *Borke* im *Wels* entdeckt hat, ist von einer sehr sonderbaren Gestalt. Er hat an seinem Kopfe, der fast nicht vom Körper unterschieden ist, zwei (vermuthlich vier) sehr grosse rundliche Saugblasen, welche dicht an einander liegen, die ganze Breite des Kopf erfüllen, und mit doppelten wulstigen Rändern, wie mit Augennestern versehen sind. Der äussere Wulst ist nach der Zeichnung dunkler als der innere, und gefleckt, beide aber etwas gestrahlt. Mitten zwischen ihnen kann sich der Scheitel in eine zapfen- oder schlauchähnliche kegelartige Erhöhung verlängern, welche am Ende eine Mündung hat, unten sich in den Kopf ausbreitet, und mit ihm zusammenfliesst. Man dürfte auf den Gedanken gerathen, als wenn dieser Wurm von dem oben-beschriebnen Welsbandwurme nicht wesentlich verschieden wäre, allein man hat bei jenem die kegel-förmige Verlängerung des Scheitels und seine Mündung nicht bemerkt; auch sind bei eben demselben die Glieder grösser im Verhältniss des Körpers und deutlich organisirt. Hier ist diess nicht, sie gleichen mehr undeutlichen Runzeln, und nach der Vergrösserung sind sie viereckig, fünfmal breiter als lang, mit abgestumpften Ecken. Der Hals ist ungegliedert und punktirt.

“Es waren wenige, äusserst kleine Bandwürmer im Verhältniss gegen den grossen Fisch, kleiner als im Hecht. Sie befanden sich mehr in der Gegend des Afters, krümmten sich im Leben beständig, und sogen sich mit den Saugwarzen an ihrem eigenen Körper an. Das Ausstrecken und Einziehen des Rüssels wie auch das Aufblähen der Saugwarzen, gab ein angenehmes Schauspiel.”

Schrank (1788) devoted a two line diagnosis to each of the two forms reported by Goeze from *Silurus glanis*. The second form he called *Taenia glanis*. His diagnosis adds nothing to the data given by Goeze and Batsch. Gmelin (1790) gave Latin diagnoses for *Taenia siluri* and *Taenia percae* form  $\beta$ . These diagnoses are of no value except to show that he regarded these two forms reported by Goeze to be two distinct species.

Rudolphi (1810:116-119) summed up the knowledge of this species and for the first time called attention to the fact that Goeze's two forms



constituted but a single species. Rudolphi apparently had a personal knowledge of this species and hence his data carry much more weight than do those of some of the other writers immediately preceding him. His description together with his synonymy is here quoted:

"*Taenia osculata* Goeze.

"*Taenia: osculis rostellique apice concavis, parte antica capillari, articulis quadratis planis, margine majorum integerrimo.*

Goeze Naturg. p. 415. Tab. 33. fig. 9. 10. *T. osculata.*

Idem ib. p. 416. Tab. 33. fig. 11-14. *Taenia alternatim transverse lineata.*

Batsch Bandw. p. 209. n. 45. fig. 146. 147. *T. osculata.* p. 157. n. 16. fig. 80. 82. *T. siluri.*

Schrank Verzeichn. p. 47. n. 141. *T. osculata.* n. 142. *T. glanis.*

Gmel. Syst. Nat. p. 3080. n. 82. *T. siluri.* ib. p. 3079. n. 77. *T. percae* β.

Tabl. Encycl. t. 49. fig. 4. 5. (ic. Goez.) *T. siluri.* fig. 6-9. (ic. Goez.) *T. alternans.*

Zeder Naturg. p. 353. n. 40. *Halysis siluri.* n. 41. *Hal. transverse-lineata.*

"Hab. in *Siluri Glanidis* parte intestini praesertim media, saepe tamen etiam inter priorem. Goezius Iulio, ego Majo, reperimus.

"Descr. Vermes pauci a Comite de Borke reperti exigui, duo a Goezio observati duodecim pollices longi; mei, copiosissimi, pollicem ad pedem et quod excurrit longi, antice capillares, postice lineam ad sesquilineam lati.

"*Caput* discretum, subglobosum, exiguum, *Oscula*, uti caput totum, quam in specie praecedente multo minora, concava, profunda, ostio exiguo, ut in illa sita saepeque simul in conspectum venientia. *Rostellum* intermedium, brevissimum, osculum quintum, sed minus et plerumque magis protrusum refert. *Corporis* plani et tenuis pars antica in verme tam pollicari quam pedali capillaris, mox tantum rugosa vel incisa videtur *colli* speciem sistens, mox autem articulis distinctis iisque tenuissimis, forma variis, moniliformibus, oblongis et rugaeformibus interjectis, constat; pars reliqua sensim increscens, articulis tandem quadratis, satis aequalibus, margine laterali rectiusculo, integerrimo. Articulus ultimus rotundatus, fere semper emarginatus. Cujusvis articuli majoris media pars *ovarium*, sive maculam oblongam, pellucidam continet, quae neque anteriorem, neque posteriorem articuli marginem attingit. A quolibet ovario *linea transversa* ad alterum articuli marginem lateralem, ordine plerumque alterno, non tamen certo, excurrit. *Linea longitudinalis*, qualis in specie praecedente, in hac non conspicua.

"Substantia vermis tenuis, at firma et duriuscula, ideoque in aqua non pro speciei praecedentis more intumescit vel gelatinosa fit. Vermibus utriusque speciei aequae magnis, prioris volumen multo majus.

"Obs. 1. Hujus et praecedentis discrimen, quo minus conjungantur, nimis magnum esse, cuique observationem illi adjectam legenti, vel utramque recentem aut spiritu vini servatum comparanti patebit.

"Obs. 2. Me speciem a Comite de Borke detectam et Goezio osculatam dicam, cum altera hujus auctoris specie (transversim lineata) conjunxisse forsan miveris, sed utrique collum non articulatum et tenue adscribitur, quale praecedenti

semper deest, et Borkius, qui Taeniolas suas in Glanidis intestinis crassis repperit, nonnisi partem vermium summam offendisse videtur, dum articulos rugas potius referre asserit, quod de hujus tantum parte antica valet. Goezius vermes majores repperit et ejusdem icon (fig. 11.). Taeniam integram sistens, bona est. Capitis vero icones neque Borkiana neque Goeziana laude dignae sunt. Zederus, verme licet non viso, alteram Goezii speciem rescindendam esse, recte praedixerat.

"Obs. 3. Müllerus de Taenia ocellata, nobis n. 21. dicta, loquendo, Taeniam transverse-lineatam Goezii ab illa lineolarum lateralium defectu solo forsan differre, suspicatus est, quo Gmelinus commotus, qui Taeniam nostram oscellatae varietatem fingeret, sed osculata toto coelo diversa, et rostello solo jam distingui potest.

"Obs. 4. Omnes quidem Taeniae osculatae sunt, nostra autem (uti et praeedens) κατ'ἑξοχὴν ita vocari potest, cum osculo quinto quasi instruat, et oscula valde profunda sint. Goezii ergo nomen conservavi, et praecedentem simili voce designavi."

Rudolphi (1810:115) also described *Taenia calycina* from *Silurus glanis*. This species he later (1819:497) came to consider as identical with *Taenia osculata*. His later observations are here given:

"Entozoologiam edendo duplicem hujus Taenia formam, mihi tum temporis constantem visam prae oculis habui, quo commotus T. calycinam mihi dictam ab osculata distinxī. Postmodum vero Gryphiae Octobri mense Siluri Glanidis quinquaginta tres libras pondere aequantis intestina examinando, Taenias plurimas reperi inter T. osculatam et calycinam et ita quidem intermedias, ut nullum amplius discrimen superesset. Tres quatuorve pedes longae collo mox longiore mox breviori utebantur; articuli lineis longitudinalibus, rarius (posteriores) etiam transversis insignes; aquae commissae quasi gelatinosae reddebantur, aliquot dies vivae conservatae. Taenia calycina ideoque rescindenda est."

Rudolphi (1819:150) gave a very brief Latin diagnosis of *T. osculata* and stated that he had collected it at Greifswald. Dujardin (1845) and Diesing (1850) added very little to the previous diagnoses and descriptions. Wagener (1854) is inaccessible to the writer hence it is impossible to review his findings. Carus (1857) gave two drawings of this form after Wagener (1854). Van Beneden (1861:165) listed this species of cestode. Riegenbach (1896) considered it a species of Ichthyotaenia but he gave no descriptive data on the species. Two drawings of the head by Wagener are reproduced (Figs. 161, 162).

Lühe (1909:30-31) gave a short descriptive diagnosis of the species and in an original figure, reproduced (Fig. 182), he showed a little of the structure of the proglottid. His diagnosis reads:

"Zirka 50 cm bis 1 m lang, bei einer grössten Breite von ca. 3 mm. Scolex mit einem kleinen scheitelständigen "Saugnapf", der mit zahlreichen, sehr hinfalligen Haken von 0,007 mm Länge besetzt ist. Proglottiden mit entwickelten

Geschlechtsdrüsen sowie auch solche mit Uterus annähernd quadratisch. Genitalöffnung in der Mitte des Gliedrandes. Cirrusbeutel klein, kaum über den Dotterstock nach innen hinausragend; das Knäuel des Vas deferens stark quergestreckt, vom Cirrusbeutel bis an die Medianlinie reichend. Hodenbläschen sehr zahlreich, das ganze Mittelfeld der Proglottis einnehmend. Vagina ohne Sphincter. Uterus jederseits mit etwa 6-8 schlanken, sich etwas verzweigenden Seitenästen. Kalkkörperchen anscheinend spärlich.

"Im Darm von *Silurus glanis* L."

La Rue (1911:475) listed this as a little known species of *Proteocephalus*.

The above diagnosis by Lühe and his drawing of the inner structure of the proglottid furnish the only available data on the anatomy of this species. Unfortunately his drawing and description fail to show many of the details which one might desire. If his interpretation of the structures there found are correct then one must consider that so far as the arrangement and character of the generative organs are concerned this species must belong with the genus *Proteocephalus*. The presence of the minute spines on the fifth sucker is not in strict accord with the writer's ideas of this genus. At first glimpse one is caused to think of the spines on the head of the members of the genus *Acanthotaenia* and is led to inquire whether this species does not have its place in that genus. However, since the *Acanthotaenia* are found thus far only in the Varanidae, a family of lizards, it seems that this species can not have its closest relatives there. Since its host is a member of the genus *Silurus* and since this genus harbors several species of cestodes of the genus *Monticellia* one must consider the possibility of its belonging with the latter. Here, it seems to the writer, this species will eventually be placed but at present all the data, meager tho they are in details, place it in the genus *Proteocephalus*.

#### TAENIA SIMPLICISSIMA Leidy

1887: <i>Taenia simplicissima</i>	Leidy	1887:22
1891: <i>Taenia simplicissima</i>	Monticelli	1891
1896: <i>Ichthyotaenia simplicissima</i>	Riggenbach	1896:267
1911: <i>Proteocephalus simplicissimus</i>	La Rue	1911:475

This species was first described in a very superficial way by Leidy (1887) who besides the wholly inadequate species description figured the head and the outline of the proglottids in two drawings. Monticelli (1891) without comment included this species in a list of forms which somewhat resembled his *Tetracotylus* (*Taenia*) *coryphicephala*. Riggenbach (1896) included this form in a list of species of *Ichthyotaenia*.



He did not discuss his reasons for so doing. La Rue (1911) inadvertently included this form among a list of species of *Proteocephalus*.

Leidy's description is here quoted:

"*Taenia simplicissima*.—Head small, unarmed, truncate; bothria spherical, terminal, occupying the four angles; neck very long, nearly or as wide as the head, body gradually widening to the posterior third and then tapering; anterior segments transversely linear, subsequently reversed disklike, gradually longer and wider, then campanulate and gradually becoming longer and narrower. Generative apertures and ova unobserved. A number of specimens from the Cod, *Gadus callarias*, up to 20 lines by 1 mm. where widest. Two only of the specimens retained the head."

The only reliable data in the description and the drawings have to do with the head and the form of the proglottids. Not even the genital pores were noted. Furthermore so far as the writer is able to find out no investigator since Leidy has seen or described this parasite of the cod. Nor is it likely that Leidy's specimens remain for he did not save many of them and many of those which he preserved have since been destroyed hence a re-examination of his specimens seems unlikely. Since the host is a purely marine fish and since no undoubted species of *Proteocephalus* are known to come from marine hosts the writer holds it highly improbable that this form is a species of *Proteocephalus*. Other than the fact that it has four sessile suckers and inhabits a fish it certainly has no claim for a place in the genus *Proteocephalus*. The species is therefore deleted from the list of *Proteocephalus* species and Leidy's original name for it is retained.

#### TAENIA BELONES Müller

The writer has examined the statements of Rudolphi (1819:175) in regard to *Taenia belones* and he agrees with Monticelli (1891) and Riggenbach (1896) in believing that this form does not properly belong in the genus *Proteocephalus*. Monticelli (1891) expressed the view that this species is identical with *Bothriocephalus belones* Dujardin. Riggenbach (1896) apparently accepted Monticelli's statement.

#### TAENIA POLLACHII Rathke

Rudolphi (1819:175) gave a short statement in regard to this form but evidently he did not regard it as a well known species. Monticelli (1891) thought it very probable that this form was identical with *Abothrium gadi* Van Beneden. Riggenbach (1896) apparently accepted this view. The writer has found no reason for thinking that this form is a species of *Proteocephalus*.

## CHOANOSCOLEX ABSCISUS (Riggenbach 1896) La Rue

[Fig. 151]

1896: <i>Ichthyotaenia abscisa</i>	Riggenbach	1896:193-210
1911: <i>Choanoscolex abscisus</i>	La Rue	1911:479

Specific Diagnosis: Characters of genus. Worms small, 25-30 mm. long, breadth up to 0.765 mm. Number of proglottids as many as 70. Head somewhat conical with a fold of tissue at the base at times partly covering the suckers. Apex of head flattened. Maximum breadth of head 0.476 mm. No rostellum, no fifth sucker. Suckers large oval, 0.306 mm. long by 0.136 mm. broad. First proglottid longer than broad. Tenth proglottid 0.476 mm. broad by 0.102 mm. long. Segments near middle of worm broader than long or nearly quadrate. Last proglottid 1.02 mm. long by 0.765 mm. broad. Proglottid margins straight, posterior corners rounded. Last proglottid with bluntly rounded end.

Sexual organs as in genus. Genital aperture situated at end of anterior  $\frac{1}{3}$ - $\frac{1}{5}$  of the proglottid. No genital papilla. Testes, about 100 in number, 0.054 by 0.045 mm. in size, arranged in a single layer between vitellaria. Coils of vas deferens voluminous. Coils of ductus ejaculatorius few. Cirrus swollen, with large lumen. Cirrus-pouch large, pear-shaped, muscular, reaching nearly to middle of segment. Length of cirrus-pouch 0.34 mm. Vagina anterior or posterior to cirrus-pouch. Lumen of first part of vagina large. Receptaculum seminis present. Ovary bilobed, posterior, unbranched. Vitellaria lateral, follicular. Uterus a median tube with many lateral outpocketings. Eggs, 0.021 mm. long by 0.016 mm. broad.

Habitat: *Silurus* sp., Rio Paraguay, South America.

This species was described by Riggenbach (1896) as a species of *Ichthyotaenia*. La Rue (1911:479) established for it a new genus, *Choanoscolex* and made this species the type of the new genus.

The material was collected by Dr. Ternetz in Paraguay, 1894. The following description is based on the work of Riggenbach (1896). Riggenbach considered this form to be a species of *Ichthyotaenia* and his comparisons are made with species of that genus rather than with *Corallobothrium*.

The worm is small being 25-30 mm. in length. It is made up of about 70 proglottids whose form varies according to the age. The scolex (Fig. 151) varies from the usual shape in being somewhat conical instead of spherical and in having at the base of the cone a fold of tissue or a mantle which may be partially drawn over the suckers. The tip of the cone is flattened. The maximum breadth of the head is 0.476 mm.,

the breadth of the flattened apex of the cone 0.255 mm. The suckers which are separated from each other by a small zone only are very large in proportion to the size of the head. The shape is oval or at times triangular. Their length is about 0.306 mm. and their breadth about 0.136 mm.

The head reaches its greatest breadth, 0.476 mm., at the point where it passes over into the neck of medium length and a breadth of 0.348 mm. First proglottids are very narrow transverse bands. The tenth proglottid is about 0.476 mm. broad by 0.102 mm. long. As in most species the length of the proglottid increases with age more rapidly than the breadth. The twentieth proglottid has a length of 0.153 mm. Proglottids near the middle of the worm are broader than long or quadrate. The last proglottid is 0.765 mm. broad by 1.02 mm. long. Margins of the proglottids are straight and the posterior corners of the proglottids are rounded. Except for the slight elevation in the region of the genital opening, the geometrical form of the proglottid is not disturbed. The last proglottid is rounded off at the posterior end.

Riggenbach (1896:196-199) described the cuticula, parenchyma, musculature, and nervous system. These structures are typical for Proteocephalids. He did not describe the musculature of the head. In the head the small space between the suckers is almost completely filled with vessels of the excretory system. The four main vessels are bent inward as they enter the head. A circular anastomosis behind the suckers could not be demonstrated. In the short apical region of the head the vessels are never capillaries and an apical capillary plexus such as is found in *Corallobothrium lobosum* does not occur. Riggenbach was not able to find a direct connection of the vessels of the head or of the plexus with the exterior. Posterior to the suckers the main excretory vessels pass to the lateral fields of the neck in a course that is perpendicular to the longitudinal axis of the body, then they bend posteriad, decrease in size and extend throughout the strobila as nearly straight narrow tubes. In the region of the cirrus-pouch and vagina the dorsal vessel passes above and the ventral vessel below these organs. The excretory vessels lie mesad of the vitellaria and the lateral nerve trunks. At the posterior part of each segment the main excretory vessels are connected by a transverse anastomosis. In the region of the transverse anastomosis are canals which connect the main vessels with the exterior. These canals arise directly from the main vessels and not from a capillary network. The point of opening to the exterior is on the surface near the posterior angle of the proglottid. In the posterior part of the end-proglottid the four main vessels join together to form a small blad-



der or reservoir. This reservoir opens in the middle of the rounded posterior margin of the end-proglottid.

The genital aperture is marginal, irregularly alternating, situated at the end of the anterior  $\frac{1}{3}$  to  $\frac{1}{5}$  of the proglottid. A genital papilla is not present tho the margin of the genital sinus is slightly swollen. In structure and arrangement the sexual organs agree thoroly with the general relations of *Proteocephalus*. Riggensbach mentions a *receptaculum seminis* as being new to *Ichthyotaenia* but it has been found in several species of *Proteocephalus*.

The testes number about 100. They measure 0.054 by 0.045 mm. They lie in a single layer in the medullary parenchyma, between the vitellaria and anterior to the ovaries. The vas deferens forms a voluminous knot of coils outside the cirrus-pouch. The ductus ejaculatorius forms a few coils in the cirrus-pouch and then, undergoing a change in histological structure, it passes over into the cirrus, the basal part of which is much broadened to form a roomy ovoidal vesicle. The cirrus somewhat resembles the cirrus of *Monticellia malopteruri* (Fritsch). Riggensbach did not see the protruded cirrus. The cirrus-pouch is a large pear-shaped and muscular sac extending into the segment perpendicular to the margin. Its length is about 0.34 mm. Since the ripe proglottids measure about 0.70-1.0 mm. broad the cirrus-pouch must reach from  $\frac{1}{3}$  to  $\frac{2}{5}$  across the proglottid.

The vagina opens into the common genital sinus anterior or posterior to the cirrus-pouch. In old proglottids the beginning part of the vagina is swollen into a sac nearly as large as the cirrus-pouch but in young proglottids the diameter of the vagina is uniform. In its course to the middle of the proglottid it describes an arc, then it bends sharply and passes to the interovarial space in a spiral or sinuous course. The convolutions of vas deferens are crossed by the vagina only when the latter opens anterior to the cirrus-pouch. A receptaculum seminis is present near the mid-piece of the ovary. This is more than a broadening of the vagina at this point for in Riggensbach's drawing there is shown a change in the histological structure of the vaginal wall. The relations of the organs with the interovarial space is similar to that in species of *Proteocephalus* and need not be discussed here. The bilobed ovary is in the posterior region of the proglottid. The lobes are unbranched saclike structures united by a mid-piece from which the oviduct arises. The vitelline glands are lateral follicular structures extending the full length of the segment. They occupy a broad zone laterad to the excretory vessels and the nerve trunks. The uterus is a median longitudinal tube with a large number of lateral outpocketings on either side. The uterine eggs are 0.021 mm. long by 0.016 mm.

broad. "The elongated shell is very thin and surrounds in part the yet undifferentiated egg-cell with the yolk-cells, in part the cell-groups which are the results of the first development stages." Evidently Riggensbach saw no embryos.

In life the heads of typical species of *Proteocephalus* are extremely variable in form passing with considerable rapidity from one contraction state to another. By the contraction of longitudinal muscles extending into the apex of the head the suckers may be drawn down out of sight within the inflated neck region but there are no folds of tissue at the base of the head within which the head may retreat. In the species just described this fold of tissue within which the suckers are partially withdrawn seems to be a constant feature of the scolex. Thus the head differs from heads of species of *Proteocephalus*. At first one notes certain similarities with the scolices of species of *Corallobothrium*. Further consideration of the structure of the two types of heads convinces one that they are not alike. The head of a *Corallobothrium* is greatly flattened anteriorly and the suckers are directed anteriorly. At the margins of the flattened apical region are numerous folds and lappets which form a corolla-like sheath about the suckers. In this species the head is conical and the suckers are directed outward. In *Corallobothrium lobosum* Riggensbach (1896) found a small muscle-cross connecting each dorsal sucker with the ventral sucker opposite it. Riggensbach did not see such a structure in his sections of the heads of *Ichthyotaenia abscisa*. It is doubtful if it occurs in any other genus known at present to belong in this family.

This species may be considered as forming a transitional stage between *Proteocephalus* and *Corallobothrium*. This view is supported by the appearance of heads of plerocercoids of an unknown species of *Corallobothrium* found encysted in the liver of *Ameiurus melas* and *A. nebulosus* from the Illinois river. The heads of these plerocercoids possessed but a few simple folds of tissue enveloping a part of the head. When alive the heads were somewhat conical, not flattened on the apex as in preserved heads of the adult worms. However, a marked difference between these heads and the heads of *Choanoscolex abscisa* may be noted. In the plerocercoids the suckers are plainly paired, two dorsal and two ventral, while in this species the head is but slightly flattened dorso-ventrally and the suckers are not plainly paired. This species does not belong in the genus *Corallobothrium* or *Proteocephalus*.

The foregoing descriptions of species of *Proteocephalus* are briefly summarized in and supplemented by the following comparative table.

Comparative Table of Selected Characters of Proteocephalus Species

Characters	<i>Proteocephalus flicollis</i> (Rud.)	<i>P. esocis</i> (Schneider)	<i>P. agonis</i> (Barbieri)	<i>P. exiguus</i> La Rue	<i>P. pusillus</i> Ward
Strobila	35 mm. long x 0.8 mm. broad. Reported longer by other authors	10-47 mm. long x 0.7 mm. broad at widest part	30-40 mm. long x 0.5 mm. broad	9-15-25-38 mm. long x 0.425-0.646-0.8 mm. broad at widest part	30-50 mm. long x 0.35 mm. broad at widest part
Neck	Narrow, 1 mm. long	2-5 mm. long	3 mm. long x 0.14 mm. broad. Limits poorly defined	2-4-7-10 (?) mm. long x 0.1-0.2 mm. broad	1-1.5 mm. long x 0.21 mm. broad
First proglottids	0.075-0.08 mm. long x 0.2 mm. broad	0.17 mm. long x 0.37 mm. broad	Broader than long	Longer than broad or nearly square	Broader than long
Mature proglottids	0.18 mm. long x 0.37 mm. broad	0.39 mm. long x 0.68 mm. broad	Longer than broad. 0.58-0.62 mm. long x 0.33-0.37 mm. broad	Longer than broad but smaller than ripe proglottids	Longer than broad
Ripe proglottids	0.48-0.66 mm. long by 0.425 mm. broad	.....	Nearly quadrate, length and breadth about .5 mm	Longer than broad, 0.935 mm. long x 0.595 mm. broad, —0.68 x 0.56, —1.19 x 0.46 mm.	0.84-1.4 mm. long x 0.18-0.35 mm. broad
Head	Short, broad	0.9-0.121 mm.	0.14 mm. broad, 0.105 mm. thick	Somewhat globular, flattened dorsoventrally. 0.12-0.16-0.17 mm. broad	Spheroidal, 0.3 mm. broad, 0.26 mm. long
Suckers (the four)	Nearly round, 0.042-0.055 mm. in diameter	Shallow, weak, 0.05 mm. in diameter. Aperture 0.026-0.032 mm. in diameter	Circular	0.058 mm. broad x 0.069-0.085 mm. long. Aperture 0.04 mm. in diameter	Slightly elongated, deep, muscular, 0.14 x 0.11 mm.
Fifth sucker	Not present	Not present	Not present	Muscular, functional, diameter 0.037-0.048 mm.	Well developed, muscular, 0.06 mm. in diameter
Genital pore, location on margin of proglottid	Near middle	Near middle	Near middle	Near middle	At end of first third to two-fifths
Cirrus-pouch, size	0.13 mm. long x 0.032-0.04 mm. broad	0.23-0.25 mm. long	Long, (0.25 mm., estimated)	0.289-0.34 mm. long	0.095-0.106 mm. long, 0.53-0.06 mm. broad



Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>Proteocephalus filicollis</i> (Rud.)	<i>P. esocis</i> (Schneider)	<i>P. agonis</i> (Barbieri)	<i>P. exiguus</i> La Rue	<i>P. pusillus</i> Ward
Cirrus-pouch, length of into breadth of segment.	3-4 times	About 2 times	About 2 times	About 2 times	3-4 times
Ductus ejaculatorius	In several coils	Straight (?)	Nearly straight	Straight	In 1 or 2 coils
Testes, number	75-90	44-52	100	35-54	44-60-70
Testes, size	0.055-0.062 mm. x 0.035-0.045 mm.	0.05-0.09 mm. in diameter	Diameter 0.031-0.038 mm.	Diameter 0.04-0.05 mm.	Testes oval, 0.06-0.09% x 0.04-0.05 mm.
Testes, arrangement*	In 2 layers	In 2 partial layers	Number of layers?	In 1 layer	In 2 layers.
Vagina, relation of, to cirrus-pouch	Anterior to cirrus-pouch	Anterior to pouch	Anterior to pouch	Anterior to pouch, crossing middle of latter	Lies anterior to, but never crosses, cirrus-pouch
Uterus, pouches on each side	5-7-8	.....	4-6-8	9-14	10-14-16
Embryo, size	0.027 mm	.....	.....	0.019-0.021 mm.	.....
Eggs, number and size of membranes	Three membranes. Outer one 0.05-0.075 mm. in diameter, inner 0.027 mm.	.....	Number? Egg measured 0.037-0.038 mm. in diameter	Three membranes Outer one 0.038-0.06, second 0.036-0.046 mm. in diameter	.....
Additional data	Slight genital papilla sometimes present. Segmentation indistinct; hence neck of unstained specimens appear to be relatively very long	Segmentation indistinct. Specimen immature	Occurred in great numbers, 1200 in a single host	.....	Ovarian lobes pressed closely together posteriorly
Hosts	<i>Gasterosteus aculeatus</i> , <i>G. pungitius</i>	<i>Esox lucius</i>	<i>Alosa finta</i> var. <i>lacustris</i>	<i>Coregonus nigripinnis</i> , <i>C. prognathus</i> , <i>C. arcticus</i>	<i>Salmo sebago</i> , <i>Coregonus namaycush</i>
Locality	Germany; France; Ireland; Sweden; Finland	Estonia	Italy	Lake Michigan	Maine; Ontario.
Chief sources of data	Schneider (1905), the present paper	Schneider (1905), the present paper	Barbieri (1909)	Benedict (1900), the present paper	Ward (1910), the present paper

\*Testes are characteristically in a single field between vitellaria.

Comparative Table of Selected Characters of Protocephalus Species (Continued)

Characters	<i>P. pinguis</i> La Rue	<i>P. nematosoma</i> (Leidy)	<i>P. fallax</i> La Rue	<i>P. neglectus</i> La Rue	<i>P. dubius</i> La Rue
Strobila	9.0 cm. long x 1.24 mm. broad at widest part	7.6-33 cm. long x 2.25 mm. broad. (Measured when alive?)	10 cm. long x 1.2 mm. broad at widest part	Length not known, 0.153 mm. broad at widest part	4 cm. long x 0.8-1.2 mm. broad at widest part
Neck	3-7 mm. long x 0.2-0.25 mm. broad	Very short or none, 0.25 mm. broad	2 mm. long (balsam mounts), 6 mm. (in glycerine), 0.076-0.136 mm. broad	.....	1.8-3.5 mm. long x 0.085-0.14 mm. broad
First proglottids	Very short, 0.05 mm. long x 0.25 mm. broad	Proglottids 25 mm. from head 0.175 mm. long x 1-2 mm. broad	0.17-0.3 mm. long x 0.126 mm. broad	.....	0.05 mm. long x 0.2 mm. broad
Mature proglottids	Nearly quadrate, about as large as ripe proglottids	Quadrate or barrel-shaped	0.34 mm. long x 0.34-0.46 mm. broad	.....	Quadrate, broader than long, or longer than broad. 1.02 mm. long x 0.34 mm. broad. 0.59 mm. long x 0.68 mm. broad
Ripe proglottids	Nearly quadrate or longer than broad. 0.595 mm. square-0.73 mm. long x 0.595 mm. broad	Posterior segments 0.5-0.75 mm. long x 2-2.5 mm. broad	Longer than broad, rarely 1.36 mm. long x 1.19 mm. broad	Range from 0.5 mm. long x 0.93 mm. broad to 0.75 mm. long x 1.53 mm. broad	Usually longer than broad, 1.19 mm. long x 0.68 mm. broad, 0.68 mm. long x 1.02 mm. broad
Head	Conical, flattened dorso-ventrally, 0.33 mm. broad, 0.22 mm. thick, 0.2-0.25 mm. long	Rounded quadrate, 0.25-0.375-0.5 mm. broad	Somewhat globose, 0.15-0.2 mm. broad, 0.105-0.15 mm. thick	.....	Variable in shape, 0.127-0.212 mm. broad, 0.10-0.14 mm. long
Suckers (the four)	Cup-shaped, deep, muscular, 0.095-0.105 mm. in diameter, aperture 0.06 x 0.07 mm. in diameter	Hemispherical, 0.125-0.175 mm. in diameter	Rounded, 0.064-0.085 mm. in diameter. Aperture about 0.04 mm.	.....	Round or irregular, with deep cavity. Suckers measure 0.069-0.08 mm. in diameter
Fifth sucker	Functional, 0.05-0.075 mm. in diameter	None present, but there is a papilla at the apex. (Can papilla be a sucker?)	Functional, about 0.058 mm. in diameter	.....	0.026-0.037 mm. in diameter
Genital pore, location on margin of proglottid	Near middle	Marginal	Near middle	Near middle	Near middle
Cirrus-pouch, size	0.13-0.14 mm. long, 0.05-0.06 mm. broad	.....	0.196-0.255 mm. long in mature and 0.37-0.42 mm. long in ripe proglottids	When contracted 0.18-0.265 mm. long, 0.08 mm. broad, normally 0.34 mm. long.	0.265-0.37-0.425 mm. long, 0.07-0.08 mm. broad

Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>P. pinguis</i> La Rue	<i>P. nematosoma</i> (Leidy)	<i>P. fallax</i> La Rue	<i>P. neglectus</i> La Rue	<i>P. dubius</i> La Rue
Cirrus-pouch, length of into breadth of segment.	3-4 times	.....	2-3 times	3-4 times	2-2½ times
Ductus ejaculatorius	Nearly straight	.....	In 1 or 2 sinuous curves	Straight	Straight
Testes, number	54-70	.....	30-35.	75	55-60
Testes, size	Testes oval, 0.05 x 0.04-0.05 mm	.....	Diameter 0.037-0.06 mm.	Diameter 0.042-0.064 mm.	Diameter 0.063-0.075 mm.
Testes, arrangement*	In 1 layer	.....	In a single layer	In a single layer	In 2 partial layers
Vagina, relation of, to cirrus-pouch	Anterior but opens dorsal to cirrus-pouch	.....	Anterior; may cross inner end of cirrus-pouch, usually runs past inner end of pouch	Anterior, crosses middle of cirrus-pouch	Anterior crosses middle of cirrus-pouch
Uterus, pouches on each side	10-14	.....	6-8	7-9	7-10-12-14
Embryo, size	0.016-0.018 mm.	Ova measured 0.28-0.032 mm. (over all?)	Diameter 0.031-0.0336 mm.	Diameter 0.026-0.0265 mm.	Diameter 0.032 mm.
Eggs, number of membranes	.....	.....	Three membranes. Middle one 0.036-0.041 mm. Outer one not measured	Three membranes. Outer one 0.042-0.047 mm.	Three membranes. Middle one 0.042-0.053 mm.
Additional data			Description based on fragments		
Hosts	<i>Esox reticulatus</i> , <i>Esox luctus</i>	<i>Esox reticulatus</i>	<i>Coregonus fera</i>	<i>Trutta fario</i>	<i>Perca fluviatilis</i>
Locality	Maine; Michigan, Wisconsin	Fish were brought to Philadelphia markets	Switzerland	Switzerland	Switzerland
Chief sources of data	The present paper	Source? Leidy (1888 & 1890)	Kraemer (1892), the present paper	The present paper	Zschokke (1884), the present paper

\*Testes are characteristically in a single field between vitellaria.



Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>Proteocephalus cernuae</i> (Gmelin)	<i>P. percae</i> (O. F. Müller)	<i>P. longicollis</i> (Zeder)	<i>P. salmonis-umbrae</i> (Monticelli)	<i>P. torulosus</i> (Batsch)
Strobila	40 mm. long x 1.5 mm. broad at widest part	2-20 cm. long x 1.1-1.5-2 mm. broad at widest part	2-20-46.4 cm. long x 1-2-2.25 mm. broad	30-60 mm. long x 1 mm. broad	6.6-60 cm. long x 1.2-2.25 mm. broad at widest part
Neck	1.7-2 mm. long x 0.3-0.39 mm. broad	3-10 mm. long x 0.17-0.5 mm. broad	3.2 mm. long x 0.3 mm. broad	.....	2-3 mm. long x 0.2-0.3 mm. broad
First proglottids	0.085 mm. long x 0.425 mm. broad	Usually broader than long, 0.085-0.102 mm. long x 0.255-0.34 mm. broad	0.43 mm. long x 0.71 mm. broad	.....	Much broader than long
Mature proglottids	Always broader than long, 0.476 mm. long x 0.816 mm. broad	Broader than long, 0.255-0.34 mm. long x 1.19-1.3 mm. broad	Measurements at end of first third of worm, 0.53 mm. long x 0.99 mm. broad	Longer than broad	Broader than long
Ripe proglottids	Usually broader than long, 0.68-0.85 mm. long x 1.309-1.51 mm. broad	Broader than long, 0.42-0.85 mm. long x 1.1-1.7 mm. broad	At posterior end of worm, 1.03 mm. long x 0.83 mm. broad	.....	0.29-1 mm long x 1.3-2.5 mm. broad
Head	Flattened anteriorly, and dorsoventrally, 0.291-0.316 mm. broad, 0.1 mm. long	Short, broad, flattened dorsoventrally, 0.192-0.357 mm. broad, 0.17-0.238 mm. thick	0.43 mm. broad	.....	Large, swollen, flattened dorsoventrally, 0.48-0.6 mm. broad, 0.3 mm. thick
Suckers (the four)	Almost globular, heavily muscled, deep. Diameter 0.064-0.09 mm.	Muscular, deep. Diameter 0.085-0.1-0.137 mm.	Circular in outline. Diameter 0.12-0.14-0.18-0.19 mm.	.....	Circular, deep. Diameter 0.18-0.2 mm
Fifth sucker	Diameter 0.024 mm.	Diameter 0.033-0.06 mm.	Half the size of the others	Not present	No trace of fifth sucker found in sections of head
Genital pore, location on margin of proglottid	Near middle	Near middle	At end of first fourth	At end of first two-fifths to three-fifths	Near middle
Cirrus-pouch, size	Slender, 0.185-0.228 mm. long	0.34-0.47 mm. long	Short, 0.11 mm. broad	Long	0.255 mm. long x 0.085 mm. broad
Cirrus-pouch, length into breadth of segment	4½-5-6-7 times	2½-3 times	4-5 times	About 2 times	4-6 times

Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>Proteocephalus cernuus</i> (Gmelin)	<i>P. percae</i> (O. F. Müller)	<i>P. longicollis</i> (Zeder)	<i>P. salmonis-umblae</i> (Monticelli)	<i>P. torulosus</i> (Batsch)
Ductus ejaculatorius	In 1-3 coils	Straight	.....	.....	Few or no coils
Testes, number	70	50-60	25 (Probably more)	Numerous	100-110
Testes, size	Diameter 0.085-0.13 mm.	0.05-0.095 x mm.	Diameter 0.09 mm.	.....	Diameter 0.16-0.08 mm.
Testes, arrangement*	In 1 layer	In 1 layer	In 2 lateral fields(?) In 2 layers	No free mid-field. Lay- ers(?)	In 2 layers, one filling whole dorsal field
Vagina, relation of, to cirrus-pouch	Anterior, never crosses cirrus-pouch	Anterior, crosses cirrus- pouch near middle	Anterior	.....	Dorsal or anterior, not crossing pouch
Uterus, pouches on either side	6-8-9-12	4-5-9	3	6	3-4
Embryo, size	Diameter 0.0212-0.0265 mm.	Diameter 0.019 mm.	Unripe eggs measure 0.0156-0.0196 mm. in di- ameter	.....	Diameter 0.021 mm.
Eggs, number and size of membranes	Three membranes. Sec- ond one 0.037-0.04 mm. in diameter	Three membranes. Sec- ond one 0.0264-0.029 mm., outer one 0.031- 0.037 mm. in diameter	.....	.....	Three membranes. Outer one 0.055 mm., middle one 0.033 mm. in diam- eter
Additional data	Vitellaria usually farther removed from margin of proglottid than is com- mon for species of this genus	.....	.....	.....	Septa of uterus fleshy, appearing branched when sectioned
Hosts	<i>Acerina cernua</i>	<i>Perca fluviatilis</i> , <i>perca norvegica</i> , <i>Coregonus la- arctus</i>	Salmonoid fishes, see list in description of species	<i>Salmo salvelinus</i>	Cyprinidae. See list giv- en in species description
Locality	Prussia; Lake Balaton(?)	Germany; Finland; Swe- den	Germany; Finland; Switz- erland	Switzerland; Germany	France; Germany; Fin- land; Switzerland; Aus- tro-Hungary
Chief sources of data	The present paper	Schneider (1902; 1903; 1905), the present paper	Von Linstow (1891)	Zachokke (1884), Lühe (1909)	Krämer (1892), the pres- ent paper

\*Testes are characteristically in a single field between vitellaria.

Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>P. macrocephalus</i> (Creplin)	<i>P. amblolitis</i> (Leidy)	<i>P. perpleurus</i> La Rue	<i>P. singularis</i> La Rue
Strobila	40 cm. long x 1-1.8 mm. broad at widest part	28-41 cm. long x 2-2.5 mm. broad at widest part	15.5 cm. long x 1.7 mm. broad at broadest part	17-25 (?) cm. long x 0.9-1 mm. broad at widest part.
Neck	5-7 mm. long x 0.1-0.25 mm. broad	Short, broad 0.25-0.45 mm.	0.5 mm. long. Broad and thick, almost as broad as head	2-3 mm. long x 0.1-0.2 mm. broad
First proglottids	0.022 mm. long x 0.33 mm. broad	0.022-0.028 mm. long x 0.344 mm. broad	Much broader than long	0.117-0.02 mm. long x 0.255 mm. broad
Mature proglottids	0.4-0.63 mm. long x 1-1.2 mm. broad	Usually broader than long. 0.5-1.2 mm. long x 1.5-2.5 mm. broad	0.595 mm. long x 1.7 mm. broad	0.34-0.37 mm. long x 0.85 mm. broad
Ripe proglottids	Length may exceed breadth. 0.9-2.08 mm. long x 0.49-1.2 mm. broad	About same size as mature proglottids	Quadrate or longer than broad. 1.1 mm. long x 1.02 mm. broad to 1.75 mm. long x 0.51 mm. broad	Quadrate or longer than broad. 0.85 mm. square, 0.51 mm. long x 0.86 mm. broad. 0.9-1.0 mm. long x 0.68 mm. broad. Old spent proglottids as much as 2.0 mm. long x 0.4 mm. broad
Head	Globose, flattened dorsoventrally. 0.28-0.3-0.32 mm. broad, 0.15-0.16 mm. thick	Somewhat pyramidal or globose, deeply grooved, 0.57-0.88 mm. broad	Spheroidal, flattened dorsoventrally, deeply grooved. 0.663-0.714 mm. broad, 0.425-0.51 mm. long	Small, deeply grooved; at apex a slender protuberance, not a rostellum. 0.25-0.3 mm. broad, 0.2-0.22 mm. long
Suckers (the four)	Almost spherical. Diameter 0.095-0.106 mm. Aperture 0.05-0.06 mm.	Circular or oval, deep. 0.3-0.4 mm. long	Circular or oval, deep. 0.34-0.459 mm. long x 0.255-0.272 mm. broad	Shape variable, always with pointed apex, weakly muscled. 0.13-0.17 mm. long x 0.17-0.19 mm. broad
First sucker	Vestigial, deeply set in tissues of head	Vestigial, deeply set in tissues of head	No trace of fifth sucker found in sections of head	No trace of fifth sucker found in sections of head
Genital pore, location on margin of proglottid	Near middle	At end of first fourth	At end of first fourth or half	At end of first fourth or half
Cirrus-pouch, size	0.16 mm. long	0.4-0.5-0.65 mm. long x 0.15-0.23 mm. broad	0.3-0.344 mm. long. Elongated oval in shape	Slender, 0.185-0.2-0.265 mm. long
Cirrus-pouch, length into breadth of segment	6-8 times	2½-3½ times	3-4.5 times	2½-3 times



Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>P. macrocephalus</i> (Creplin)	<i>P. ambloplitis</i> (Leidy)	<i>P. perplexus</i> La Rue	<i>P. singularis</i> La Rue
Ductus ejaculatorius	In 1 or 2 coils	In many coils	In 1-3 coils	In few or no coils
Testes, number	100-120	75-100.	135-155	75-80-90
Testes, size	0.063-0.074 mm. x 0.042-0.063 mm.	Diameter 0.05-0.65 mm.	0.069 x 0.037 mm.	0.07-0.1 x 0.04-0.06 mm.
Testes, arrangement*	In a single layer	In 1 or 2 irregular layers	In 1 layer	In 1 layer
Vagina, relation of, to cirrus-pouch	Anterior, opening almost dorsal to that of cirrus-pouch	Anterior	Anterior, not crossing cirrus-pouch	Anterior, not crossing cirrus-pouch
Uterus, pouches on either side	7-11-14	15-20	20-25	20-25
Embryo, size	Spheroidal or ovoidal. Diameter 0.017-0.019-0.021 mm.	Diameter 0.0168-0.018 mm.	Usually ellipsoidal. 0.013-0.014 x 0.014-0.0156 mm.	Diameter 0.014-0.0156-0.0168 mm.
Eggs, number and size of membranes in diameter	Three membranes. Middle one 0.026-0.036 mm. in diameter	Three membranes. Outer one 0.036-0.043, middle one 0.022-0.024 mm. in diameter	Three membranes. Outer one 0.024-0.036 mm., middle one 0.019-0.03 mm. in diameter	Three membranes. Outer one 0.027-0.033 mm., middle one 0.026-0.031 mm. in diameter
Additional data	Remarkable for its very short cirrus-pouch	Sphincter vaginae very long and very thick. All vitelline follicles lateral	Sphincter vaginae short, thick, situate at end of long dilatation. Some vitelline follicles along posterior margin of pro-lottid	Sphincter vaginae weak, situate about 0.1 mm. from genital sinus, followed by dilatation. Vitellaria lateral. Excretory vessels very sinuous
Hosts	<i>Anquilla chrysopa</i>	<i>A. Ambloplitis rupestris</i> , <i>Micropierus salmoides</i> , <i>M. dolomieu</i> , <i>Amita calva</i>	<i>Amita calva</i> . <i>Lepisosteus platostomus</i>	<i>Lepisosteus platostomus</i>
Locality	Europe; Eastern United States	New York; Michigan; Minnesota	Illinois	Illinois
Chief sources of data	Schneider (1905), the present paper	Leidy (1887), Benedict (1909), the present paper	The present paper	The present paper

\*Testes are characteristically in a single field between vitellaria.

Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>Proteocephalus sulcatus</i> (Klaptocz)	<i>P. pentastoma</i> (Klaptocz)	<i>P. fossatus</i> (Riggenbach)	<i>P. skorikowi</i> (v. Linstow)
Strobila	6.8 cm. long x 1.52 mm. broad in widest part	2.8 cm. long x 1.19 mm. broad at widest part	35-40 mm. long, breadth unknown	20 cm. long x 3.75 mm. broad at widest part
Neck	No neck	No neck. First proglottids appear 0.06 mm. back of sucker margins	Broad, 0.85 mm. long	.....
First proglottids	Broader than long. Almost as broad as head	Much broader than long	0.135 mm. long x 0.612 mm. broad	Very short, 1.14 mm. broad
Mature proglottids	Quadrate or longer than broad. Some segments are ripe before becoming quadrate	Mid-proglottids 0.21 mm. long x 1.19 mm. broad	Quadrate	0.95 mm. long x 3.75 mm. broad. (Measured at middle of worm. Not stated that proglottids are mature here.)
Ripe proglottids	Largest proglottid 2 mm. long x 1.5 mm. broad	Sixth from last proglottid 0.21 mm. long x 0.59 mm. broad. Next to last 0.31 mm. long x 0.41 mm. broad	Longer than broad	Proglottids at posterior end of worm measure 1.97 mm. long x 3.16 mm. broad
Head	Variable in shape, deeply furrowed. 0.46-1.75 mm. broad x 0.67-1.28 mm. thick, depending on state of contraction	Oval in transection, deeply furrowed. 0.973 mm. broad x 0.83 mm. thick	Conical with depression at apex. Head 0.714 mm. broad	Short, 0.67 mm. broad
Suckers (the four)	Rounded, deep, 0.25 mm. in diameter	Oval or round in outline, 0.5 mm. in diameter	Diameter 0.34 mm.	Diameter, 0.25 mm.
Fifth sucker	No fifth sucker	A true fifth sucker, 0.085-0.1 mm. in diameter	No fifth sucker	Present, 0.13 mm. in diameter
Genital pore, location on margin of proglottid	At end of first third	Near middle	A little anterior to middle	Posterior to middle
Cirrus-pouch, size	0.2-0.25 mm. long. (Measured on drawing made to scale.)	.....	Elongated oval in shape, 0.3 mm. long	.....
Cirrus-pouch, length into breadth of segment	4 times	.....	3 times	5-6 times

Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>Proteocephalus sulcatus</i> (Klaptocz)	<i>P. pentastoma</i> (Klaptocz)	<i>P. fossatus</i> (Riggenbach)	<i>P. skorikowi</i> (v. Linstow)
Ductus ejaculatorius	In several coils	.....	In a few coils	.....
Testes, number	200	70-100	120-150	Numerous, judging from drawing about 70-100
Testes, size	.....	.....	Diameter 0.05 mm.	Diameter 0.053-0.083 mm.
Testes, arrangement*	Number of layers? Tend to form two lateral fields	Number of layers? Tend to form two lateral fields	Number of layers? Irregularly scattered over dorsal field	Number of layers? Irregularly scattered over dorsal field
Vagina, relation of, to cirrus pouch	Posterior	Posterior	Anterior	Anterior
Uterus, pouches on either side	10-12 (drawing)	Immature	Many	6-8
Embryo, size	.....	.....	.....	0.021-0.023 mm. in diameter
Eggs, number and size of membranes	Number of membranes? Eggs measure 0.016 mm. in diameter, 0.029 mm. long	.....	.....	Two membranes, outer one 0.027 mm. in diameter
Additional data	Cirrus, when protruded, long and slender, thicker at base. On atrial side the vitellaria are pierced by genital canals so that small follicles lie dorsal and ventral to these ducts Series of genital pores on right alternating with smaller series on left side	.....	Small genital eminence present	Vagina forms many coils anterior to the ovary. Ovary consists of two groups of slender club-shaped bags. Cirrus 0.141 mm. long
Hosts	<i>Polypterus endlicheri</i> , <i>Claroetes laticeps</i>	<i>Polypterus bichir</i>	<i>Pimelodus pati</i>	<i>Acipenser stellatus</i>
Locality	White Nile	White Nile	Rio Paraguay, S. A.	River Gürgen, Caspian Sea
Chief sources of data	Klaptocz (1906)	Klaptocz (1906)	Riggenbach (1896)	von Linstow (1904)

\*Testes are characteristically in a single field between vitellaria.



Comparative Table of Selected Characters of Protocephalus Species (Continued)

Characters	<i>P. cyclops</i> (v. Linstow)	<i>P. salvelini</i> (Linton)	<i>P. sagittus</i> (Grimm)	<i>P. osculatus</i> (Goese)
Strobila	2.5 cm. long x 0.27 mm. broad	3-5 mm. long. Breadth unknown	4.5 cm. long x 1 mm. broad at widest part	50-100 cm. long x 3 mm. broad
Neck	.....	.....	12 mm. long x 0.5 mm. broad. (Probably many small segments were overlooked.)	.....
First proglottids	.....	Indistinct, broader than long	About quadrate	.....
Mature proglottids	.....	Largest segments 1.5 mm. long x 0.75 mm. broad	Longer than broad	About quadrate
Ripe proglottids	.....	.....	Last 8 segments 1.4-1.5 mm. long x 1 mm. broad x 0.3 mm. thick	About quadrate
Head	End of head rounded. Size not stated	Rounded in front, 0.3-0.4 mm. in diameter, varying with state of contraction	Thick, pointed at apex	.....
Suckers (the four)	0.15 mm. long x 0.1 mm. broad	Prominent, rather deep. 0.15-0.18 mm. in diameter. Aperture 0.1 mm. in diameter	Heavily muscled, elongated	.....
Fifth sucker	Present, 0.069 mm. in diameter	Not present	Not present	Small fifth sucker provided with minute hooks
Genital pore, location on margin of proglottid	.....	A little anterior to middle	Near middle	At middle
Cirrus-pouch, size	.....	0.26 mm. long x 0.14 mm. broad	Large and club-shaped. Cirrus quite thick	Short, scarcely reaching through the vitellaria
Cirrus-pouch, length into breadth of segment	.....	.....	.....	5-6 times

## Comparative Table of Selected Characters of Proteocephalus Species (Continued)

Characters	<i>P. cyclops</i> (v. Linstow)	<i>P. salvelini</i> (Linton)	<i>P. sagittus</i> (Grimm)	<i>P. osculatus</i> (Goeze)
Ductus ejaculatorius	.....	.....	.....	.....
Testes, number	.....	.....	.....	Very numerous, about 140 in drawing
Testes, size	.....	Prominent	.....	.....
Testes, arrangement*	.....	Situated in central region in front of rudimentary germ gland	.....	Number of layers? In dorsal field
Vagina, relation of, to cirrus pouch	.....	.....	.....	.....
Uterus, pouches on either side	.....	.....	.....	6-8
Embryo, size	.....	.....	.....	.....
Eggs, number and size of membranes	.....	.....	.....	.....
Additional data	Immature. Suckers pointed at posterior end	Immature	.....	Vagina without a sphincter

Hosts	<i>Coregonus maraena</i>	<i>Cristivomer namaycush</i>	<i>Cobitis barbata</i>	<i>Silurus glanis</i>
Locality	Schallsee, Germany	Lake Superior	Petersburg and Province of Novgorod, Russia	Germany
Chief sources of data	von Linstow (1877)	Linton (1897)	Grimm (1872)	Goeze (1782) Lühe (1909)

\*Testes are characteristically in a single field between vitellaria.

## OPHIOTAENIA PERSPICUA La Rue

[Figs. 10, 102]

1911: *Ophiotaenia perspicua* La Rue 1911:480

Specific Diagnosis: Characters of the genus. Length up to 36.0 cm. Maximum breadth about 2.0 mm. Head conical, flattened, divided by grooves into four quadrants. Breadth of head 0.355-0.408 mm., thickness of head as much as 0.306 mm., length about 0.270 mm. Suckers four, circular, oval or at times somewhat triangular, 0.105-0.170 mm. in maximum dimension. Cavity of sucker 0.053-0.106 mm. in diameter. Neck long, 5-7 mm. in length by 0.170-0.425 mm. broad. First proglottids short. Mature proglottids quadrate, 2.0 mm. in length and breadth, or somewhat longer than broad. Ripe proglottids measure as much as 3.8 mm. long by 1.2 mm. broad. Segmentation indistinct. Proglottids attached by full width. Surface smooth. In life and when preserved in formol specimens somewhat translucent.

Genital pore marginal, irregularly alternating, situated near middle or at end of first third of proglottid. Vagina anterior or posterior to cirrus-pouch. Testes 150-215, oval or polygonal, measuring up to 0.053-0.106 mm., situated in two fields. Vas deferens in ripe proglottids a heavy mass of coils reaching from end of cirrus-pouch to the mid-field. Cirrus-pouch 0.255-0.320 mm. long by 0.080-0.090 mm. broad. Ratio of length of cirrus-pouch to proglottid breadth 1:4 to 1:3. Cirrus slender, about 0.20 mm. long when protruded. Vagina dilated in first part, not crossing cirrus-pouch. Sphincter vaginae and receptaculum seminis present. Lobes of ovary long, flattened, irregular in outline, made up of anastomosing tubules. Oöcapt and oötype present. Vitellaria loose. Uterus when ripe with 20-30 lateral pouches on either side. Uterine pores not seen. Eggs provided with three membranes, outer one 0.045-0.100 mm. in diameter. Embryos 0.018-0.021 mm.

Habitat: *Natrix (Nerodia) rhombifer* Hallowell, (type host); Havana, Illinois, (type locality).

Type: Unaccessioned bottles in coll. La Rue, also bottle in Dr. H. B. Ward's collection. Slides of same.

The host, a very large female, was caught on the banks of the Illinois river at Havana, Illinois, and was examined for parasites July 9, 1910. From the intestine 57 cestodes and pieces were taken. Of these 42 pieces had heads attached. No strobilas were found with an end-proglottid. There were, however, a number of specimens with ripe proglottids. Because of their translucent appearance in life and when pre-



served in formol the writer (1911) has proposed the specific name *Ophiotaenia perspicua*. Other specimens of this species were furnished the writer by Mr. Herman Douthitt from *Natrix* (*Nerodia*) *rhombifer* taken in Oklahoma, June, 1910.

La Rue (1911:480) described this species in a preliminary way and made it the type of his new genus *Ophiotaenia*.

Two heads of the lot from Oklahoma measured respectively 0.374 mm. and 0.340 mm. broad by 0.27 mm. thick. The suckers measured 0.119 mm. long by 0.102 mm. broad. The neck was 0.272 mm. broad and several millimeters long. The longest worm was 135 mm. long by a maximum breadth of 1.19 mm. Specimens were mounted in toto and from them a positive determination was made. The longest specimen of the preserved type material measured 36.0 cm. in length by a maximum breadth of 2.0 mm. The neck is long, slightly broader than the head and not easily distinguished from the segmented portion following. The first proglottids are very short. About 16.0 cm. from the head the proglottids are quadrate, length and breadth being about 2.0 mm. These proglottids are mature. At 26.0 cm. from the head the proglottids begin to increase in length and to decrease in breadth. The second from the last proglottid measures 3.8 mm. long by 1.2 mm. broad. These proglottids are ripe. An examination of other specimens of the lot shows a considerable variation in dimensions. Proglottids are attached by their full width. The margins of the strobila are smooth, almost without indentations at the junction of the proglottids. As a consequence the segmentation is indistinct so that without staining and clearing the proglottid limits are made out with difficulty even with a microscope. The proglottids are rectangular in shape, rarely oval. The surface of the worm is sometimes thrown into shallow longitudinal furrows. No transverse furrows are noted. In life and when preserved in formol the specimens are translucent from which character is derived the specific name.

The head is somewhat conical in shape, slightly flattened dorso-ventrally and marked off into four quadrants by grooves which extend from the basal region to, or nearly to, the apex. Each quadrant bears at its thickest and broadest region a sucker which opens outward and slightly forward. The apex does not exhibit a circular depression or a fifth sucker. The head varies in breadth from 0.255 mm. to 0.408 mm. This dimension slightly exceeds the thickness and length. A head 0.357 broad measured 0.306 mm. in thickness, while a head 0.408 mm. broad was about 0.270 mm. long.

The suckers show also considerable variation in size and shape. In general they are nearly round or oval in outline with shallow cavities.

However some of them appear nearly triangular. They measure 0.105-0.170 mm. in diameter. In the smaller ones the effect of contraction is very plainly shown by the deeper cavity and by the thickened muscular wall. The diameter of the sucker opening varies from 0.053 to 0.105 mm. A vestigial fifth sucker resembling that of *O. filaroides* is found imbedded in the tissues of the head. The neck is always long, 5 to 7 mm., and its breadth is subject to considerable variation, from 0.170 to 0.425 mm.

Since this study is based upon toto preparations almost exclusively, the excretory, nervous and muscular systems were not studied carefully. The excretory system is made up of coiling trunks and anastomosing branches in the head and extreme anterior neck region. In the proglottids two pairs of main lateral excretory vessels can be made out.

The sexual organs (Fig. 102) in their character and relations are typical of the snake Proteocephalids. The genital sinus is marginal, irregularly alternating and situated near the middle, or it may be as far anterior as the end of the first  $\frac{1}{3}$  of the proglottid. It is marked by a slight elevation which becomes more pronounced in the more elongated proglottids. The vagina and cirrus open into the common shallow genital sinus. The vagina lies either anterior or posterior to the cirrus-pouch but more frequently anterior. Rarely the vagina is dorsal to the cirrus-sheath.

The testes are very numerous, 150-215. They are arranged in two fields, leaving a free median zone. In elongated mature and ripe proglottids the testes are oval or even polygonal. They measure as much as 0.053 by 0.106 mm. It is to be noted that the testes tend to occur in groups of 2, 3 or 4. In these cases the limiting membranes of the testes touch each other. The vasa efferentia may be clearly seen in some toto preparations. They much resemble the vasa efferentia in other species. The vas deferens in young proglottids is nearly straight. It arises in the middle of the proglottid and extends to the cirrus-pouch which it enters. As the proglottid becomes older the vas deferens becomes longer and more and more coiled until in mature and ripe proglottids it forms a heavy mass of coils lying between the cirrus-pouch and the middle of the segment. When filled with deeply stained spermatozoa this mass becomes very prominent. Upon entering the cirrus-pouch the vas deferens becomes the ductus ejaculatorius, which is coiled several times before passing over into the heavier-walled cirrus. The cirrus is somewhat swollen but is much smaller than in *Crepidobothrium gerrardii*, *O. calmettei*, or *O. grandis*. When protruded it is slender and of even diameter from tip to base. Its length protruded is about 0.200 mm. This measurement is taken from a specimen from Oklahoma. The

cirrus-pouch is more slender than in several other species of *Ophiotaenia*. In mature and ripe proglottids it measures from 0.255-0.320 mm. long by 0.08-0.09 mm. broad. In maturing proglottids it measures about 0.25 mm. long and is considerably narrower than in ripe ones. Its length goes into the proglottid breadth 3-4 times. In mature and ripe proglottids the vagina very near its opening to the exterior has a wide but short inflated region. A sphincter vaginae has been found. In this region the vagina is richly set with gland cells. In its course to the interovarial space the vagina bends somewhat anteriad and then inward and posteriad, crossing the numerous coils of the vas deferens but not crossing the cirrus-pouch. Just before the ovary is reached the vagina is somewhat twisted or even thrown into small coils. A small receptaculum seminis can be seen in some preparations. The ovarian lobes are long flattened bodies of irregular outline. They are not solid but are made up of short heavy anastomosing tubes of irregular shape. Just back of the mid-piece of the ovary the muscular oöcapt can be noted even in toto mounts. The coils and connections of the oviduct, vitelline duct, uterine passage and lower vagina cannot be made out distinctly. An oötype and shell-gland have been seen in some preparations.

The vitellaria are loosely follicular and lateral. The paired vitelline ducts cross the ovarian lobes. The uterus in maturing proglottids is a median tube from which as the proglottid becomes older lateral pouches arise by the method that has been described for *O. filaroides* by La Rue (1909). There are 20-30 large pouches on either side and a number of smaller ones. No uterine pores have been seen. In one toto preparation the uterine passage may be traced to a point 0.29 mm. anterior to the mid-piece of the ovary where it discharges into the uterus.

The eggs are furnished with three membranes, an outer one which is smooth, thin and hyaline, a middle membrane thick and granular, and an inner thin membrane surrounding the embryo. The outer spheroidal membrane measures 0.045-0.06-0.100 mm. and the embryos are 0.018-0.021 mm. in diameter. Plerocercoids were found encysted in the intestine and liver of the host caught at Havana, Illinois.

This species is much smaller than *Crepidobothrium gerrardii* (Baird), *O. marenzelleri* (Barrois), *O. calmettei* (Barrois) and *O. trimeresuri* (Parona) in most respects tho it may exceed some of these in length. It most closely resembles *O. nattereri* (Parona), likewise from one of the Colubrinae. It has a larger head and larger proglottids and a greater number of testes than *O. nattereri*. *O. perspicua* is much larger than *O. filaroides* La Rue from *Amblystoma tigrinum* Green. Its



head is smaller, its testes are more numerous and the position of its genital pore is very different from that of *O. filaroides*. *O. perspicua* differs from *O. lönnbergii* (Fuhrmann) from *Necturus maculosus* Raf. in having a smaller head and smaller suckers and more numerous testes.

OPHIOTAENIA LACTEA (Leidy) Sp. Inq.

1855: <i>Taenia lactea</i>	Leidy	1855:443
1911: <i>Ophiotaenia lactea</i>	La Rue	1911:481

On account of the inaccessibility of Leidy's description, it is here quoted in full:

"*Taenia lactea* Leidy.—Head small, continuous with the neck, without rostellum; acetabula anterior, hemispherical, situated at the four angles. Neck moderately long. Segments anteriorly transversely oblong, posteriorly longer than the breadth, square with rounded angles. Generative apertures marginal (indistinct in the specimen.)

"HAB.—One specimen 16 inches long and  $\frac{3}{8}$  of a line wide was found in the intestine of *Tropidonotus sipedon*. In alcohol the specimen contracted one-half the original length and widened to 1 line."

La Rue (1911:481) made this a species inquirenda in his newly established genus *Ophiotaenia*. This is probably a species of *Ophiotaenia* and may be the same as the species reported by the writer from *Natrix rhombifer*. Unfortunately the writer has had as yet no opportunity to make a study of any *Ophiotaenia* from *Natrix sipedon* and hence is unable to form an opinion of the likelihood that the two species of host harbor the same parasites. Leidy's description is too inadequate to permit a careful determination of the position of his form and since his specimens could not be had by the writer for study his species is considered to be a species inquirenda. Further research may indicate its proper position.

## OPHIOTAENIA FILAROIDES La Rue

[Figs. 26-28, 43-46, 103-105]

1909:	<i>Proteocephalus filaroides</i>	La Rue	1909:17-49
1911:	<i>Ophiotaenia filaroides</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Worms attenuate, small, thin, flat. Length 80-110 mm., maximum breadth about 0.80-0.90 mm. Color white, in life somewhat translucent. Strobilation not evident. Intersegmental furrows shallow. Surface smooth. Scolex globose, flattened dorsoventrally, with conical apex, without apical depression or fifth sucker. No rostellum. No spines. Head not marked by furrows. Breadth of head 0.366-0.46 mm. Suckers deep, muscular, oval in outline, maximum dimension 0.165-0.184 mm. Neck narrow, 3-4 mm. long. First proglottids 0.30-0.36 mm. broad by 0.10-0.17 mm. long. Mature proglottids quadrate or longer than broad. Ripe proglottids from 1.6 mm. long by 0.8 mm. broad to 4.0 mm. long by 0.75 mm. broad. End-proglottid present. Musculature weak. Parenchyma coarse, filled with large fat globules.

Genital organs typical of genus. No genital papilla. Genital pore marginal, irregularly alternating, situated at end of first fifth of proglottid. Testes 0.05-0.06 mm. in diameter, 70-114 in number, arranged in two lateral fields. Ductus ejaculatorius with a few coils in cirrus-pouch. Cirrus weakly muscled, slender, cylindrical, 0.2-0.3 mm. long when protruded. Cirrus-pouch about 0.22 mm. long by 0.11 mm. broad. Vagina always anterior to cirrus-pouch, not crossing latter. Weak sphincter vaginae and small receptaculum seminis present. Ovarian lobes thin, alate, composed of anastomosing tubules. Organs of interovarial space typical of genus. Vitellaria with large follicles. Uterus, when developed, with 25-35 lateral pouches on either side. Uterine pores 8-12. Eggs with three membranes. Outer one 0.035-0.100 mm., second, 0.030 mm., embryo 0.021 mm. in diameter.

Habitat: Intestine and rectum of *Amblystoma tigrinum* (Green) [type host], Nebraska (type locality) and Kansas.

Type: Unnumbered alcoholics in collection of La Rue and slides of same. Autotype in collection of Dr. H. B. Ward.

This species was first described by La Rue (1909:17-49) as *Proteocephalus filaroides*. So far as the writer has been able to find out no one else has worked on the species. La Rue (1911:481) included this species in a list of species of *Ophiotaenia*.

This material was obtained from *Amblystoma tigrinum* (Green) caught in ponds in Nebraska, both at Crete and in Cherry County, also in a pond at Belleville, Kansas. The specimens were taken during the summers of 1907 and 1908. The data presented here are for the most part extracted from the former article (La Rue, 1909) but the data regarding the character of the fifth sucker are new.

These cestodes are attenuate, thin and flat. In life they are white, at times somewhat translucent. The chain presents no evident strobilation, for the proglottids are closely joined by their full breadth and the intersegmental furrows are shallow. There are no longitudinal or transverse furrows in preserved specimens. The strobila measures 80-110 mm. in length by a maximum breadth of 0.80-0.90 mm. The scolex (Fig. 26) is globose, flattened somewhat dorsoventrally, and possessing a smooth conical apex in which there is no depression nor fifth sucker. There is no rostellum and no spines. The surface of the head is usually smooth and but rarely marked by furrows. The head measures 0.366-0.40 mm. broad. Four oval suckers are borne at the broadest part of the head. They measure 0.165-0.184 mm. in the maximum dimension. The suckers have deep cavities and their musculature is well developed.

As in many other species of this group which possess no functional fifth sucker there is in the tissue below the surface of the apex of the head a structure which the writer formerly called an endorgan. This structure appears as a small mass of tissue surrounded by a definite membrane. The mass of tissue contains a few nuclei and a few scattered fibers which may be muscle fibers. In the adult this structure is about 0.063 mm. long by 0.034 mm. broad. It has no opening to the exterior. Two histological drawings of the adult organ are to be found in a previous paper (La Rue 1909, Figs. 13 and 17). In the plerocercus this structure is much larger than in the adult. This fact was pointed out in the author's paper of 1909 and figures were given to show the difference in size. These figures have been reproduced (Figs. 27, 28). If sections through the head of plerocercoids of this species be examined one notes that the endorgan has many points in common with the functional fifth sucker. There is a sucker cavity communicating with the exterior, a basement membrane, muscle fibers (sub-cuticular and radial). The musculature about the organ is also like that about other suckers. These histological features are shown in drawings which are reproduced (Figs. 43-46). This structure is, however, undergoing a marked modification. The sucker cavity is completely or partially filled with a granular mass of apparently the same texture as that which makes up the greater bulk of the sucker itself. The radial muscles are no longer arranged in such beautiful order as in other suckers but they seem to



be twisted and pressed out of the regular position and spread far apart by the granular mass. Radial muscle fibers showing the most typical arrangement are to be seen in figure 45. Nuclei are plainly seen and these are figured as the larger oval black spots. The drawing of the endorgan (Fig. 43) is made from a head cut in a frontal or sagittal plane. It shows the opening to the exterior, the basement membrane and the cuticular lining of a part of this opening. It also shows the cut ends of the muscle fibers next to the basement membrane. Some of these same features may be well seen in other drawings (Figs. 45 and 46) which are drawn from transverse sections of other heads.

It is evident from the structures here described and the drawings which illustrate them that this organ is in reality a sucker. It is a sucker which evidently comes to a certain state of development in which as pointed out by the writer in his former paper on this species (La Rue 1909:25), it is larger than the other suckers. The relative sizes of this organ are shown in drawings reproduced (Figs. 27, 28) from the former paper. This enlargement is due to a hypertrophy characterized by the presence of granules. Altho the stages succeeding this hypertrophy have not been followed out it is plain that the hypertrophy is succeeded by an atrophy of the tissues. Since the granules are not present in the adult organ they must disappear either as a result of streaming out of the sucker opening before that is closed or they may be absorbed by the organism. The sucker opening and the sucker cavity and all traces of the cuticula, outer basement membrane, and muscles about the sucker cavity are obliterated by the time this organ is found in the adult cestode head. Thus the sucker loses all connection with the exterior. It retains its limiting basement membrane, some of its nuclei and perhaps a few scattered muscle fibers. The conclusion is then that this endorgan, or muscle-plug as Johnston (1909 et seq.) has called it, is a vestigial fifth sucker. That the writer was dealing with the plerocercoids of this species is attested by the facts brought out by his feeding experiments (La Rue 1909) in which he fed plerocercoids taken from the flesh of *Amblystoma* to other uninfected *Amblystoma* and the latter became heavily infected with the cestode *Ophiotaenia filaroides*.

The narrow neck is 3-4 mm. long. This is followed by a region of short proglottids which gradually become longer and broader. The increase in length is more rapid than the increase in breadth hence the proglottids change progressively from broader than long to quadrate and then to longer than broad. The youngest proglottids measure 0.30-0.36 mm. broad by 0.10-0.17 mm. long. Ripe proglottids measure 1.6 mm. long by 0.8 mm. broad and in some cases as much as 4.0 mm. long

by 0.75 mm. broad. An end-proglottid with a rounded posterior end may be present, but it is lost with the first ripe proglottids.

The musculature of the body is weakly developed. This is particularly true of the longitudinal muscles which lie between the cortical and medullary layers of the body. In the head the excretory system is made up of coils of small anastomosing vessels which are connected with the two pairs of main lateral vessels extending through the length of the strobila. In the strobila both pairs of lateral vessels lie within the dermo-muscular sheath. The genital canals, cirrus-pouch and vagina, always pass between the dorsal and ventral excretory vessels. The latter are connected with the exterior by numerous branches which discharge on the dorsal or ventral surface more frequently than on the margin of the segment. Regularly situated foramina secundaria do not exist. A transverse excretory commissure uniting the ventral vessels in the posterior part of the proglottid has been observed. The meshes of the parenchyma are coarse, forming numerous large spaces. In material prepared by ordinary methods this tissue appears to be nothing more than abnormally loose parenchyma. When fresh material is stained with "Sudan III" or is treated with osmic acid these spaces are found to be filled with large fat globules. These tests have likewise been applied by the writer to pieces of *O. lönnbergii* with similar results. Fat globules have been found in the tissues of species of *Proteocephalus* but in this case the fat globules are small. Tests have also been made on *Taenia saginata* (?), *Taenia serrata*, and *Dipylidium caninum* and in each case fats have been found. Tests for fat have not been made on the cestodes of snakes but all the species examined show the loose parenchyma with large spaces which the fat globules once occupied.

The genital organs (Figs. 103, 104, 105) are typical of the genus. A genital papilla is not present. The genital pore is marginal, irregularly alternating, and situated near the end of the anterior fifth of the proglottid. Through the genital pore the small genital atrium is connected with the exterior. Into the genital atrium both cirrus and vagina open. The vagina always lies anterior to the cirrus-pouch. The testes (Fig. 105) measure about 0.05-0.06 mm. in diameter. They number about 70-114 and they are situated in two broad fields on either side of a free median zone. They occupy a position dorsal to the uterus. A much coiled vas deferens forms a mass which extends from the cirrus-pouch to the midfield of the proglottid. This mass of coils functions as a vesicula seminalis. Upon entering the cirrus-pouch the vas deferens becomes the ductus ejaculatorius which makes 1-3 coils before passing over into the straight and weakly muscled cirrus. When protruded the cirrus measures 0.2-0.3 mm. in length. It is slender and of almost

uniform diameter from base to tip. The cirrus-pouch is weakly muscled. Its length is about 0.22 mm. and its breadth about 0.11 mm., being broadest at its inner end.

The vagina (Fig. 105) always lies anterior to the cirrus-pouch and does not cross the latter. There are no coils of vagina anterior to the interovarial space. A weak sphincter vaginae and a small receptaculum seminis are present. The lobes of the ovary are thin and somewhat alate in shape. They are made up of anastomosing tubules. The organs (Fig. 104) of the interovarial space are typical of the genus. Vitelline follicles are large and are arranged in the lateral fields as in the other members of the group. The uterus in mature proglottids is a median tube. From this tube there arise both lateral and ventral diverticula after the manner described by La Rue (1909:33-37). The lateral diverticula in fully ripe proglottids extend to the vitellaria which by this time have degenerated to a large extent. They number from 25 to 35 on either side. The ventral diverticula number about 8-12. These are short and usually pointed. In time they pierce the ventral body wall forming the uterine pores. The ventral body wall now gives way along this line of perforations thus causing a rift which extends from one end of the proglottid to the other. Through this rift the eggs are discharged. The eggs are covered with three membranes of the character usual to the group. The outer thin and hyaline membrane varies in diameter from 0.035 to 0.10 mm. This variation is due in part to the fact that when it comes in contact with the water the outer membrane swells up greatly. The second membrane is thick and granular, about 0.030 mm. in diameter. The inner membrane which closely invests the embryo is thin. The six-hooked embryo measures about 0.021 mm. in diameter. The larval form of this cestode is frequently found encysted in the abdominal viscera and body muscles of the host, *Amblystoma tigrinum*. They have also been found free in the body cavity of the same host. As yet they have not been found in an invertebrate host.

Altho this species shows marked similarities with some of the species of cestodes infesting snakes it most nearly resembles *Ophiotaenia lönnbergii* (Fuhrmann) which infests the amphibian, *Necturus maculosus* Raf. It differs from this species in size relations, in the character of the excretory vessels, and in the relations of the cirrus-pouch to the vagina. There are some minor points in which the two species from the amphibia differ from the species infesting snakes but as yet characters have not been found by which they can be separated from the genus *Ophiotaenia*. These two species certainly do not belong with the genus *Proteocephalus*.



## OPHIOTAENIA LÖNNBERGII (Fuhrmann)

[Figs. 119, 189]

1895:	<i>Ichthyotaenia lönnbergii</i>	Fuhrmann	1895:218-226
1909:	<i>Proteocephalus lönnbergii</i>	La Rue	1909:43
1911:	<i>Ophiotaenia lönnbergii</i>	La Rue	1911:481

Specific Diagnosis: Characters of the genus. Length as much as 17-19 cm. Breadth as much as 1.35 mm. Strobilation usually indistinct. Intersegmental furrows shallow. Proglottids attached by full width. Scolex globose, flattened dorsoventrally, 0.50-0.60 mm. in breadth. No rostellum, no spines, no functional fifth sucker. Suckers prominent, muscular, oval or round, deep, measuring 0.24-0.26 mm. long by 0.14-0.22 mm. broad. Opening in oval suckers 0.20 by 0.10 mm. Neck 0.375-0.54 mm. in minimum breadth, length about 2.0 mm. First proglottids about 0.5 mm. long by 0.50 mm. broad. Mature proglottids quadrate, 0.85-1.0 mm. square or longer than broad, measuring as much as 2.5 mm. long by 0.45-0.5 mm. broad. Ripe proglottids not observed. Two pairs of main lateral excretory vessels situated at some distance from lateral margins of strobila. Vessels spiral in form. Transverse commissure present in posterior end of each proglottid. Many branches extending from dorsal and ventral vessels to exterior. In head many branches of anastomosing vessels.

Genital pore marginal, irregularly alternating, situated at end of first one-third or two-fifths of proglottid. Testes 90-160 in number, round or oval, 0.05-0.08-0.12 mm. in maximum dimension, situated in two lateral fields extending laterad of excretory vessels. Midzone of proglottid not entirely free of testes. Vas deferens forming a large mass of coils posterior to cirrus-pouch. Cirrus-pouch 0.185-0.280 mm. long by 0.05-0.085-0.10 mm. broad. Ductus ejaculatorius in several coils, frequently forming a small vesicula. Cirrus not muscular, when protruded cylindrical and 0.13-0.15 mm. long by 0.045-0.05 mm. thick. Vagina anterior or posterior to cirrus-pouch. Vaginal opening sometimes dorsal to latter, but vagina never crossing cirrus-pouch. A large dilatation in vagina of some proglottids. Sphincter vaginae and receptaculum seminis present. Ovary thin, flat, lobes wedge-shaped or alate. Organs of interovarial space typical of genus. Vitellaria sparse. Uterus in past mature proglottids possessing 25-40 lateral pouches. Eggs immature in specimens observed. Yolk-mass 0.010-0.012 mm. in diameter. Egg membranes not seen. Embryos not yet developed.

Habitat: In intestine of *Necturus maculosus* Rax. Fuhrmann does not state the locality of the host from which his type specimens

came. The writer has frequently found the species in *Necturus* from Ohio and Indiana which had been brought to the laboratory for dissection. Fuhrmann's specimen was obtained from Prof. F. Zschokke who received it from Prof. R. Burekhardt.

Type: Prepared slides in collection of Fuhrmann.

Fuhrmann (1895:218-226) described and delineated this species, calling it *Ichthyotaenia lönnbergii*. Without attempting a description of the species it was referred to by La Rue (1909:43) as *Proteocephalus lönnbergii*. In a more recent paper La Rue (1911:481) pointed out that this was to be considered as a species of a new genus, *Ophiotaenia*.

This study is based on slides and alcoholics in the collection of La Rue. The material has been carefully compared with Fuhrmann's preparations of the type which Professor Ward very kindly secured for the writer's use. The material was thus found to be identical with Fuhrmann's. Reference will be made from time to time to the work of Fuhrmann (1895) from which certain data were secured.

This form is more robust than *O. filaroides*. It may reach a length of 17.0 cm. or more. Fuhrmann's specimen, an immature worm, measured 19.0 cm. The worm is thin and flat. Its breadth varies considerably. The maximum breadth in the writer's specimens was 1.275 mm. Fuhrmann's material had a slightly greater breadth. The strobilation is rarely distinct. The margins of the strobila are quite smooth. Infrequently the posterior part of the worm may show a distinct strobilation. The proglottids are attached by their full width. Transverse folds are rare but shallow longitudinal furrows are not uncommon. The scolex (Fig. 119) is somewhat globose and is flattened dorsoventrally. On it are four prominent suckers situated on its broadest part. In breadth the scolex varies from 0.50 to 0.60 mm. There is no rostellum, no spines and no functional fifth sucker. The suckers are round or oval in outline with deep cavities and a strong musculature. In length the suckers vary from 0.24 to 0.25 mm. and the breadth from 0.14 to 0.22 mm. The opening of the more oval suckers measures about 0.20 by 0.10 mm. Immediately behind the head the neck has a breadth of 0.375-0.54 mm. The first traces of segmentation occur about 2 mm. posterior to the head.

Young proglottids, according to Fuhrmann, measure 0.27 mm. in length. The first discernible proglottids in the writer's material are about 0.050 mm. long by 0.50 mm. broad. The length and breadth of the proglottids increase rapidly for a distance then the length increases while the breadth decreases. In this material the maximum breadth of 1.275 mm. was reached long before the proglottids were mature. Pro-

glottids in this region are 1.275 mm. broad by 0.30-0.40 mm. long. Mature proglottids are about 0.85-1.0 mm. square, or they may be longer than broad. Some of the elongated proglottids measure 2.5 mm. long by 0.45-0.5 mm. broad. In Fuhrmann's specimens the last proglottids were 0.7 mm. long by 1.35 mm. broad. Neither Fuhrmann nor the writer has seen the ripe proglottids. All the hosts examined by the latter had been in captivity for some time and were examined in the spring months. It may be that the parasites attain the sexually ripe condition later in the season.

The excretory system (Fig. 189) is made up of two pairs of main lateral vessels, dorsal and ventral. These are situated much farther mesad than is usually the case with this group. They take a spiral path through the tissues. From them at frequent intervals small branches pass to the dorsal and ventral surfaces. A transverse excretory commissure is present in the posterior part of each segment. In the head the main excretory vessels are connected by means of many anastomosing branches. The parenchyma resembles that of *O. filaroides*. Chalkbodies of large size are abundant, especially in the head and neck. The musculature is weakly developed.

The genital pore alternates irregularly, is marginal, and is situated at the end of the first third or two-fifths of the proglottid. Cirrus-pouch and vagina pass to the exterior between the ventral and the dorsal excretory vessels. The male organs mature first. Testes number from 90 to 160, the number varying greatly in the proglottids of the same strobila. Elongated testes measure 0.05-0.08 and even as much as 0.120 mm. in maximum dimension. The testes (Fig. 189) lie in two broad fields which extend laterad and mesad of the excretory vessels. In many proglottids an occasional testis lies in the midfield. The testes are dorsal to the uterus. In mature proglottids the vas deferens forms a large mass of coils which function as a vesicula seminalis. This mass of coils is usually situated posterior to the cirrus-pouch. It lies almost in the mid-field of the segment. The cirrus-pouch is short and broad. Its length varies from 0.185 to 0.290 mm. and its breadth from 0.050 in the case of the long slender pouches to 0.085-0.100 mm. in the shorter and thicker pouches. The cirrus-sheath is broadest at the inner end. The ductus ejaculatorius forms several coils and then it passes over into the slender cirrus. In some proglottids the ductus is dilated to form a small vesicle. The cirrus is not muscular. When protruded it is cylindrical and about 0.13-0.15 mm. long by 0.045-0.050 mm. thick. There are no coils of ductus ejaculatorius in the base of the protruded cirrus.

The vagina lies anterior or posterior to the cirrus-pouch but its opening is usually dorsal to the latter. When the vagina occupies the



position anterior to the cirrus-pouch it never crosses the latter but passes beyond it and then dips down below the coils of the vas deferens. In many mature proglottids the initial part of the vagina is greatly dilated and this dilatation extends for some distance down the length of the vagina. There are no coils of the vagina anterior to the ovary but it may lie in sinuous curves. A weak sphincter vaginae close to the external opening and a small receptaculum seminis near the mid-piece of the ovary are present. The ovary varies in shape with the state of contraction of the proglottid. It is always thin and flat and is made up of anastomosing tubules as in *O. filaroides*. In very broad but short proglottids the lobes of the ovary are long slender wedge-shaped structures the apices of which lie in the mid-field of the proglottid. In attenuated proglottids the lobes are much shortened and broader than in long proglottids, in which case the ovary may be distinctly alate in form. The organs of the interovarial space are arranged about as delineated for *O. filaroides* (Fig. 104). The vitellaria are lateral, composed of medium-sized sparse follicles. Since no ripe proglottids have been seen a well developed uterus cannot be described. In one proglottid in which a few eggs had been passed into the uterus there were from 25 to 40 lateral pouches on either side. No uterine pores have been observed. No eggs with developed embryos could be found. A few eggs which could be but poorly seen within the uterus of a toto preparation showed yolk-masses measuring 0.010-0.012 mm. in diameter. The egg membranes could not be measured. Fuhrmann saw no eggs.

This species the most closely related to *O. filarioides* can be readily distinguished from the latter by its larger strobila, larger head, larger suckers and larger testes. The excretory vessels are spiral structures in *O. lönnbergii* but straight in *O. filaroides*. The ovarian lobes are also different in size and shape. *O. lönnbergii* differs from the *Ophiotaenia* parasitic in snakes by the position of its genital pore and by the less muscular character of its cirrus. Its ovary is also of a different shape. The position of the excretory ducts is much farther mesad in *O. lönnbergii* than in any species of *Ophiotaenia* at present known from snakes.

While further investigation may prove that the species of Proteocephalids infesting Amphibia are generically different from the species infesting snakes there is at present no justification in erecting a new genus for them. Their nearest allies are among the *Ophiotaenia*, hence the writer places them in that genus.

## OPHIOTAENIA NATTERERI (Parona)

[Figs. 139, 194, 195]

1901:	<i>Ichthyotaenia nattereri</i>	Parona	1901:4-6
1908:	<i>Ichthyotaenia nattereri</i>	Schwarz	1908:17-19
1911:	<i>Ophiotaenia nattereri</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Length 75-250 mm., maximum breadth not over 1 mm. Scolex unarmed, rounded but not spheroidal, not easily distinguished from the neck. Diameter of scolex 0.240-0.250 mm. Suckers four in number, circular, cavity deep, margin thick, diameter of suckers 0.120-0.150 mm. No rostellum and no fifth sucker. Neck long, 7-8 times the length of the head. First segments broader than long, more or less indistinct. Mature proglottids nearly quadrate. Ripe proglottids longer than broad, length of same up to 2.0 mm., breadth 0.33-0.50 mm. Last proglottids readily detached. Segmentation distinct.

Genital aperture irregularly alternating, situated somewhat anterior to middle of proglottid margin. Testes 80-100, 0.042 mm. in diameter, situated in two lateral fields. Vas deferens a thick mass of coils extending even past the middle of the proglottid. Ductus ejaculatorius much coiled. Protruded cirrus slender, heavy at base, about 0.20 mm. long. Cirrus-pouch about 0.265-0.280 mm. long, extending from  $\frac{1}{3}$ - $\frac{2}{7}$  across proglottid breadth. Vagina anterior or posterior to cirrus-pouch. Sphincter vaginae present. Uterus, when fully developed, possessing 15-20 lateral pouches on either side. Eggs provided with three membranes. Outer membrane covered with fine hooklets. Eggs 0.024 mm. in diameter.

Habitat: In intestine of *Coluber* sp. from Liguria, a district of Italy. The material was collected by Parona in December, 1897.

This species was first described by Parona (1901:4-6) but the description was not accompanied by drawings. Schwarz (1908:17-19) delineated and redescribed the species, using Parona's specimens. La Rue (1911:481) included this form in a list of species of *Ophiotaenia*. The data upon which this description is based were secured from the descriptions of Parona (1901) and Schwarz (1908), and from observations made upon slides prepared from type material which Professor H. B. Ward secured from Professor Parona.

This cestode is thin and slender. Its observed length varies from 75-250 mm. and its maximum breadth is not over 1 mm. The segmentation is distinct in the posterior region. The single proglottids are thin, and somewhat translucent. The first proglottids are broader than long and their boundaries between segments are not distinct. More mature proglottids are nearly quadrate while ripe proglottids are longer than broad. The length of ripe proglottids may be as much as 2.0 mm. and the breadth 0.33-0.50 mm. The last proglottids are easily detached from the chain. The head is small and not clearly set off from the neck. It is unarmed, rounded somewhat but not spherical; its diameter is 0.24-0.25 mm. It bears four circular suckers which have a deep cavity and a thick muscular wall. The diameter of the suckers varies from 0.120 to 0.150 mm. There is no rostellum and no fifth sucker. The neck is seven or eight times as long as the head. Cuticula, musculature, nervous system and excretory system are very similar in arrangement and character to the same systems in other species of the genus.

The early developing sex organs may be seen in quadrate proglottids. The genital aperture lies somewhat anterior to the middle of the margin of the segment and it irregularly alternates from right to left. Schwarz's figure of the ripe proglottid showing the main features of the reproductive systems is reproduced (Fig. 195). The testes lie in two fields between the vitellaria, thus leaving the median zone of the proglottid free of them. They number 80-100 and measure 0.042 mm. The vas deferens forms a thick heavy coil extending from the cirrus-pouch even past the middle of the proglottid. Within the cirrus-pouch there is a very complicated mass of coils of ductus ejaculatorius. This is much more highly developed than in any other known species of *Ophiotaenia*. The cirrus when protruded is heavy at the base, more slender at the tip and about 0.200-0.210 mm. long. In preparations where it was incompletely protruded it measured 0.108 mm. long. The cirrus-pouch is 0.265-0.280 mm. long. In quadrate and oblong proglottids its length goes into the proglottid breadth from 3 to 3.5 times.

The vagina opens into the common genital pore. It may lie either anterior or posterior to the cirrus-pouch. In 12 out of 18 proglottids examined by the writer the vagina had a posterior position. At the opening of the vagina a sphincter of good size is present. The course of the vagina is nearly direct to the middle of the segment, frequently crossing the inner end of the cirrus-pouch or even lying above the cirrus-pouch for its full length. From the middle of the segment its course is directly posteriad with sometimes a single loose coil just above or anterior to the ovaries. In the interovarial space are the usual coils of the vagina, oviduct, uterine passage, and unpaired vitelline duct; here also



are the oöcapt, oötype, and shell-gland. The uterus appears in mature proglottids as a median tube from which later 15-20 lateral pouches arise on either side. The ovarian lobes are fairly dense compact masses. In many proglottids the ovary has a more elongated and pointed form than Schwarz delineates it. The vitellaria are lateral, follicular masses, reaching from the anterior end nearly to the posterior end of the segment. According to Schwarz the eggs have three membranes. The diameter of the egg is 0.024 mm. The outer membrane of ripe eggs is covered with fine hooklets or processes which terminate in small knobs. The writer was unable to observe these processes in his toto mounts. Schwarz's figure of the egg is reproduced (Fig. 194).

This species is easily differentiated from *Crepidobothrium gerrardii*, *O. marenzelleri*, *O. calmettei*, *O. racemosa*, *O. trimeresuri* and *O. grandis* by its much smaller size, and from *O. perspicua* by its slightly smaller head and suckers, by its lesser number of smaller testes, its more voluminous cirrus-pouch and its lesser number of uterine pouches. In many respects *O. nattereri* and *O. perspicua* are quite similar. *O. nattereri* has a smaller head and smaller suckers than *O. pigmentata*. Further comparisons with *O. pigmentata* can not be made because of the incompleteness of the data on the latter.

#### OPHIOTAENIA RACEMOSA (Rudolphi)

[Figs. 140, 191]

1819:	<i>Taenia racemosa</i>	Rudolphi	1819:692
(?)1819:	<i>Taenia colubri</i>	Rudolphi	1819:709
1845:	<i>Taenia racemosa</i>	Dujardin	1845:610
1850:	<i>Taenia racemosa</i>	Diesing	1850:511, in part
1898:	<i>Ichthyotaenia racemosa</i>	Barrois	1898:3
1898:	<i>Ichthyotaenia racemosa</i>	Lühe	1898:652
1908:	<i>Ichthyotaenia racemosa</i>	Schwarz	1908:28-29
1911:	<i>Ophiotaenia racemosa</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Length of strobila as much as 160 mm., breadth about 1 mm. Length of ripe proglottids about 2 mm., breadth 1 mm. Scolex easily distinguishable from strobila, breadth about 0.54 mm. Suckers four, nearly circular, 0.27-0.30 mm. in diameter. Genital organs as in genus. Testes about 100-120 in number, 0.072-0.078 mm. in diameter, located in two broad fields which tend to fuse at middle. Ductus ejaculatorius sinuous. Cirrus-pouch long, reaching nearly to middle of proglottid. Vagina anterior or pos-

terior to cirrus-pouch. Ovary voluminous, lobes somewhat winglike. Uterus possessing about twenty long outpocketings on either side. Eggs provided with three membranes. Diameter of egg 0.024 mm.

Habitat: In intestine of South American snakes of the family Colubridae, subfamily Colubrinae.

Host	Locality	Collector	Authority
<i>Coluber</i> sp.	Brazil	Natterer	Rudolphi, 1819:692
<i>Ophiomorphus miliaris</i>	Brazil*	Natterer	Diesing, 1850:511
<i>Ophiomorphus miliaris</i>	Brazil*	Natterer	Schwarz, 1908:28
<i>Ophis merremii</i>	Brazil*	Natterer	Diesing, 1850:511
<i>Ophis merremii</i>	Brazil*	Natterer	Schwarz, 1908:28

This species was first described by Rudolphi (1819:692). Since this description is not readily accessible to many workers it is quoted in full:

"*Taenia racemosa* R. n. sp. Pone Synops. n. 52.

"T. Capite obconico, collo brevi, angustissimo, articulis planis, elongatis, foraminibus marginalibus alternis prominulis. *Hab.* In intestinis *Colubri* n. 20. specimen sexpollicare et fragmenta hujus *Taenia* Natterer in Brasilia reperit.

"*Caput* antrosum dilatatum, sive obconicum, osculis orbicularibus, aut hemisphaericis, nam satis profunda videntur, anticis. *Collum* breve, angustissimum. *Articuli*, quos vidi, plani, tenues, elongati, lineam ad sesquilineam longi, tertia lineae parte latiores, foraminibus marginalibus alternis, prominentibus.

"*Ovaria* singulorum articulorum lineam mediam fere totam sibi vindicant, ad cujus latera utrinque maculae exiguae opacae ita digestae sunt, ut ovaria racemosa appareant.

"*Obs.* Caput *Taeniae* omphalodis Synops. n. 9. articuli vero T. tuberculatae n. 25. ut fragmenta, quae vidi, *Taeniam* illis intermediam reddant."

Rudolphi (1819:709) established the name *Taenia colubri* to designate a few proglottids found in *Coluber* sp., Brazil by Natterer. His exact words are here quoted:

"*Taenia Colubri*. Pone Synops. n. 140.

Fragmenta in intestinis *Colubri* n. 12. a Natterero in Brasilia reperta Museo Viennensi debeo lineam circiter longa, duodecim ad octodecim articulis constantia, latioribus quam longis, subcuneatis, angulis plus minus exstantibus, capite destituta.

"Utrum vere colubrina, an ex ave quadam deglutita forsán residua?"

Dujardin (1845:610) added nothing to Rudolphi's description. Diesing (1850:511) gave a short diagnosis of a form from the museum at Vienna which he identified as *Taenia racemosa* Rud. His description

\*Material found in Vienna Museum.

varies so widely from that of Rudolphi and his list of hosts covers such a range of families that his words are quoted in full:

"*Taenia racemosa* Rudolphi. *Caput* magnum tetragonum, acetabulis angularibus subterminalibus v. terminalibus, subovatis v. cordatis. *Collum* nullum. *Articuli* supremi brevissimi, subsequentes longiores et latiores, angulis rotundatis, ultimi longi parallelipiedi angustiores. *Penes* filiformes basi incrassati, marginales vage alterni. Longit. 2" — 1½'; latit. med. 1 — 3''; ultim. 1''.

"*Taenia racemosa* Rudolphi: Synops. App. 692—*Dujardin*: Hist. nat. des Helminth. 610.

"Habitaculum. *Ophiomorphus miliaris*, Martio. — *Eunectes Scytale*, Octobri, Februario et Junio. — *Bothrops Mararacca*, Martio et Aprili. — *Ophis Merremii*, Januario, in Brasilia (*Natterer*): in intestinis. M. C. V."

Von Linstow (1878:183) did no more than refer to Rudolphi (1819) and Diesing (1850). Barrois (1898:3) was convinced that *Taenia racemosa* Rud. belonged to the genus *Ichthyotaenia* for he had examined a head and some ripe proglottids "provenant du type primitif de Rudolphi." He did not describe the species. Lühe (1898:652) stated that *Taenia racemosa* belonged to the genus *Ichthyotaenia*. Marotel (1899:34) quoted Diesing's (1850) description of this species which he stated was too incomplete to permit a precise determination. Parona (1901:3) reported some specimens collected by Dr. Adolf Lutz from *Bothrops (Lachnis) lanceolata*, São Paulo, Brazil under the name of *Ichthyotaenia racemosa* Rud. These specimens which have been examined by the writer prove to belong to the species *Ophiotaenia calmettei* Barrois. Shipley (1905:101) reported some cestodes from *Eunectes murinus* Wagler as *Taenia racemosa* Rud. Professor H. B. Ward secured some specimens labelled with this name from Mr. Shipley. Upon examination they proved to be specimens of *Crepidobothrium gerrardii* (Baird). Schwarz (1908:28-29) secured some material from Barrois which the latter had obtained from Dr. E. von Marenzeller of Vienna. He also secured additional material from Dr. E. von Marenzeller. Upon this material he based his description of *Taenia racemosa* Rud. He did not definitely state the name of the host from which his material was collected but evidently quoted Diesing's (1850) list of hosts. La Rue (1911:481) included this form in a list of species of the genus *Ophiotaenia*.

It is possible that *T. colubri* Rud. collected by Natterer in Brazil from *Coluber* sp. is a synonym of *T. racemosa* Rud. also collected by Natterer in Brazil from a species of *Coluber*. Rudolphi's description of *T. colubri* is insufficient to place the species, nor is there any data as to exact host and locality that would fix it. Diesing (1850:558) states



that *T. colubri* was collected by Natterer in Brazil from *Ophiomorphus poecilogyrus*. He gave no descriptive data and nothing that would be of assistance in placing Rudolphi's species. Diesing's (1850) diagnosis of *Taenia racemosa* Rud. does not agree with Rudolphi's description of that species. His statements in regard to the tetragonal head, the terminal or subterminal angular suckers which are subovate or cordate fits the diagnosis of *Crepidobothrium gerrardii* but not that of *Ophiotaenia racemosa*. The latter species has orbicular suckers. Likewise Diesing's statements that there is no neck, that the first proglottids are very short, following ones larger and broader, with rounded angles, the last proglottids long parallelopipeds and somewhat narrow agree much better with the descriptions of *C. gerrardii* than with that of *O. racemosa*. Diesing's form was considerably larger than Rudolphi's. No completely protruded cirrus was noted in the writer's material of *C. gerrardii* hence the cirri of the two forms cannot be compared. Moreover, Diesing lists *Eunectes scytale* as a host of *Taenia racemosa*. *Eunectes scytale* is a synonym of *Eunectes murinus*, a species in which *C. gerrardii*, but no other Proteocephalid, has been found. It seems probable therefore that Diesing's diagnosis of *Taenia racemosa* was based on the material from *Eunectes murinus* (*scytale*).

A further analysis of Diesing's list of hosts of *Taenia racemosa* shows that besides the Boidae, represented by *Eunectes murinus*, the Colubridae are represented by two species and the Viperidae by one species. From this evidence it seems probable that Diesing's *Taenia racemosa* must have included several species, for among the species of Ophiotaenia from snakes which have been adequately described in recent years no species has been found in hosts belonging to different families. A list of these species, their hosts, and their distribution is found elsewhere. Another fact to be remarked about these Proteocephalid species from snakes is that the individuals which infest the Boidae are larger than the individuals of the species which infest the Viperidae and these in turn are larger than those that infest the Colubridae. By the term size the writer means size of head, size of suckers, breadth of neck, breadth and length of proglottids and length of strobila. In certain of these characters the writer's general statement fails but, considered in a broad way, it is true. This is an additional reason for supposing that Diesing included several species under the one name *Taenia racemosa*.

Concerning hosts of *Taenia racemosa* Schwarz (1908:28) says: "Als Wirte werden angegeben: *Ophiomorphus miliaris*, *Ophis Merremii*, *Bothrops jararacca* (for mararacca) und *Eunectes scytale*, Schlangen, die in Brasilien vorkommen". This seems to be but a restatement

of Diesing's list of hosts. Nowhere does Schwarz state definitely the exact host from which his specimens were taken. A study of his description in comparison with other species from snakes shows that his specimens are most closely related to the species from Colubrinae yet they are distinct from any of those species. It seems then quite probable that his specimens came from one of the Colubrinae, *Coluber* sp. and possibly *Ophiomorphus miliaris* or *Ophis merremii*. They surely did not come from Eunectes, and it is highly improbable that they came from Bothrops, one of the Viperidae. The emended list of hosts of *Taenia racemosa* then contains these names, *Coluber* sp., *Ophiomorphus miliaris* and *Ophis merremii*. Further questions regarding Schwarz's *Taenia racemosa* arise. Is his species identical with Rudolphi's *Taenia racemosa*? Could Schwarz have had any of Rudolphi's type material? At the writer's request Professor Ward wrote to Professor E. von Marenzeller at Vienna for information concerning the specimens of *Taenia racemosa* which he had sent to Barrois and to Schwarz. Professor von Marenzeller replied that all of Rudolphi's types were in the Museum at Berlin. It is therefore impossible that Schwarz or Barrois had Rudolphi's type specimens for examination and the question of the identity of Schwarz's *Taenia racemosa* and Rudolphi's species of that name remains open and must so remain until Rudolphi's types are re-examined, if they still exist. Meanwhile the writer assumes that the *Taenia racemosa* of Schwarz and Rudolphi are identical.

Schwarz's material all came originally from the Museum at Vienna, some directly through von Marenzeller, and some through von Marenzeller to Barrois, then from Barrois to Schwarz. As hosts he mentioned four species of South American snakes two of which have been ruled out in the above discussion, leaving either or both *Ophis merremii* and *Ophiomorphus miliaris* as probable hosts. If the specimens were from *Ophis merremii* they were probably collected by Natterer in Brazil.

The following description is based on the work of Schwarz (1908). The observed length of specimens was 160 mm., length of ripe proglottids 2 mm. and the breadth of the same 1 mm. The scolex (Fig. 140) is readily distinguished from the strobila. It bears four nearly circular suckers which measure 0.270-0.300 mm. in diameter. The scolex has a diameter of 0.540 mm.

The sexual organs (Fig. 191) agree in arrangement with the genital organs of other Ophiotaenia. The testes are of exceptional size, 0.072-0.078 mm. in diameter, appearing as large spheres. They are not limited to the side fields but are scattered irregularly through the whole area of the segment. The testicular field is not interrupted at the anterior or posterior margin of the segment. Testes number about 100-120. The

ductus ejaculatorius takes a sinuous course through the cirrus-pouch but it forms no coils. The cirrus-pouch lies perpendicular to the longitudinal axis of the proglottid and reaches almost to the median line of the same.

Female organs are as in other members of the genus. The vagina opens either anterior or posterior to the cirrus-sheath. The ovary is voluminous, bilobed, joined at the middle by a mid-piece. The ovarian lobes are somewhat plumper in form than are those of *O. marenzelleri*. The uterus forms about 20 long diverticula on either side. In Schwarz's drawing (reproduced Fig. 191) the genital pore is marginal and at the end of the first third of the proglottid. The eggs are round and have three membranes. No hooklets are to be found on the outer membrane. Schwarz does not state whether the diameter of 0.024 mm. is the diameter of the entire egg or of the embryo.

*Ophiotaenia racemosa* is a much smaller species than *Crepidobothrium gerrardii*. Its head and suckers are smaller, the proglottids shorter and narrower. The form of the suckers is greatly different in the two species. *O. racemosa* differs from *O. calmettei* in its smaller head, smaller suckers, in the distribution of testes and in the number of uterine pouches. *O. racemosa* is likewise much smaller than *O. marenzelleri* and *O. grandis* in length, breadth, size of head, and size of suckers. It also has fewer testes. *O. racemosa* differs from *O. timeresuri* in being somewhat smaller. Its chief differences lie in the position of the testes and in the character of the cirrus and vagina. *O. racemosa* differs from *O. pigmentata* in having larger suckers. *O. pigmentata* is too poorly described to furnish more diagnostic differences. *O. racemosa* differs from *O. nattereri* and *O. perspicua* in having a larger head, larger suckers, a different arrangement of testes, and smaller proglottids.



## OPHIOTAENIA PIGMENTATA (von Linstow)

[Fig. 160]

1908:	<i>Ichthyotaenia pigmentata</i>	von Linstow	1908:85
1911:	<i>Ophiotaenia pigmentata</i>	La Rue	1911:481

Von Linstow (1908) described this species from a specimen which Edward Jacobson had collected in Java (Semarang). La Rue (1911: 481) put this form in the genus *Ophiotaenia*. Unfortunately the specimen was immature so von Linstow's description is necessarily incomplete. His description reads:

*"Ichthyotaenia pigmentata*, n. sp.—Aus der Schlange *Psammodynastes pulverulentus* Fisch.—Darm.

Länge 32mm., Breite vorn 0.51mm., hinten 1.78mm.; ein sehr lange Strecke ist ungegliedert, nur der letzte 2.5mm. lange Theil zeigt deutliche Proglottidenbildung; es ist nur ein noch völlig entwickeltes Exemplar vorhanden. Der Scolex ist abgerundet und nicht breiter als die folgende Strecke; die Länge des Scolex beträgt 0.57 mm.; die kreisrunden Saugnäpfe messen 0.18mm.; ein Rostellum und Haken fehlen. Die Glieder am Hinterende sind 0.13mm. lang; ihre Breite beträgt 1.1mm., die Dicke 0.25mm. Die Cuticula ist 0.0052mm. dick und trägt an ihrer Aussenseite einen 0.0065mm. dicken Stäbchenbesatz. Die Muskulatur ist stark entwickelt und man unterscheidet 6 verschiedene Muskelarten, 1, Ring- und 2, Längsmuskeln in dünnerer Lage unter der Cuticula; an Parenchymmuskeln 3, äussere, 4, innere Längsmuskeln, letztere bestehen aus Muskelbündeln, 5, Dorsoventral; und 6. Transversalmuskeln. In jedem Querschnitt erkennt man etwa 20 Längsgefässe; die Hauptlängsnervenzstämme verlaufen  $1/5$  des Querdurchmessers der Proglottide vom Rande entfernt; massenhaft finden sich dunkel pigmentirte, meistens eiförmige, durchschnittlich 0.026mm. lange und 0.021mm. breite Kalkkörperchen. Nur in den letzten Proglottiden findet man eine Anlage der Geschlechtsorgane, besonders deutlich ist jederseits nach innen vom Nerv der rundliche Dotterstock; trotz der geringen Entwicklung der Geschlechtsorgane ist es zweifellos dass die Art zu *Ichthyotaenia* gehört".

This is probably a species of *Ophiotaenia*. The presence of lateral vitellaria removes it from the genus *Oöchoristica*. It must, however, be placed in the list of incompletely described species.

## OPHIOTAENIA TRIMERESURI (Parona)

[Figs. 106-108, 141, 142, 192, 193]

1898: <i>Taenia trimeresuri</i>	Parona	1898:7-11
1898: <i>Ichthyotaenia trimeresuri</i>	Lühe	1898:652
1908: <i>Ichthyotaenia trimeresuri</i>	Schwarz	1908:33-35
1911: <i>Ophiotaenia trimeresuri</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Length up to 105 mm. Maximum breadth 0.75-1.5 mm. Scolex unarmed, without rostellum, broader than neck, breadth 0.75 mm. Suckers prominent, hemispherical, muscular, 0.16-0.25 mm. in diameter, situated anteriorly. No fifth sucker. Neck short, three times length of head, breadth 0.25-0.5 mm. First proglottids broader than long. Mature proglottids quadrate or longer than broad. Angles of proglottids not prominent. Strobilation indistinct.

Genital pore situated near middle of proglottid margin, irregularly alternating in position. No genital papilla. Genital sinus if present very shallow. Testes 100-108 in number, measuring 0.063 by 0.027 to 0.080 by 0.027 mm., situated in two fields not near vitellaria. All testes anterior to ovary. Mass of coils of vas deferens not large. Ductus ejaculatorius much coiled. Cirrus muscular. Many coils of ductus ejaculatorius in base of protruded cirrus. Cirrus-pouch about 0.270-0.330 mm. long by 0.136 mm. broad. Ratio of length of cirrus-pouch to proglottid breadth 1:4 or 2:5. Vagina anterior or posterior to cirrus-pouch, not crossing same. Lumen of vagina variable in size. Sphincter vaginae present. Lobes of ovary flattened, elongated, narrow. Vitelline follicles small. Uterus when fully developed with 20-30(?) lateral pouches. No ripe eggs observed.

Habitat: In the intestine of *Trimeresurus formosus* (type host); Island of Mentawai, East Indies (type locality).

Type: Specimens in Professor C. Parona's collection labelled "*Arynchotaenia trimeresuri* Par., *Trimeresurus formosus*, (Mentawai)." Also two toto preparations of the same material in the collection of Professor H. B. Ward.

Parona (1898:7-11) first described and figured this species without discovering its relation to the Proteocephalidae. Lühe (1898:652)

stated that this species belonged to the *Ichthyotaenia*. In a footnote he says, "Herr Prof. Parona hat mir die Original-exemplare der Art in uneigennützigster Weise zur Verfügung gestellt, so dass ich die Zugehörigkeit derselben zu der Gattung *Ichthyotaenia* feststellen konnte." Schwarz (1908:33-35) had no specimens of this species for examination. He rewrote Parona's description but was able to add nothing new. He believed this form to be a species of *Proteocephalus* and called attention to the fact that the lower part of the uterus in Parona's drawing was probably the ovary and that the testes would be found in the anterior region of the proglottid where they were frequently difficult to see. La Rue (1911:474) stated that this species belonged with the genus *Ophiotaenia* and gave a few of its characters.

Thanks to Professor H. B. Ward who secured this material from Professor Parona for the purpose of this study the writer has been able to give this species a more careful description than has hitherto been attempted. The material consists of about a half dozen pieces among which no head could be found. This material is labelled "*Arynchotaenia trimeresuri* Par., *Trimeresurus formosus* (Mentawei)". From it two toto preparations were made. These together with the alcoholics and Parona's original description form the basis of the following description.

In the material at the writer's disposal the head, neck and first proglottids were missing. The pieces measured 10, 20, 60 and 70 mm. long by a maximum breadth of about 1.0 mm. Parona in a table gave data concerning the length and breadth of five specimens with heads and five without. The length of those with heads ranged from 12 to 50 mm. and the maximum breadth from 0.75 to 0.1 mm. while the headless specimens measured 33-105 mm. in length by a maximum breadth of 0.75-1.5 mm. The scolex is spheroidal, has neither hooks nor rostellum, and is broader than the neck. Its diameter is about 0.75 mm. The suckers are prominent and are situated in the anterior part of the head. They are hemispherical, strongly muscular, and have a diameter of 0.16-0.25 mm. The aperture of the sucker is 0.11-0.16 mm. Parona's drawings of the scolex are reproduced (Figs. 141, 142).

The neck is about three times as long as the scolex. Its breadth varies from 0.25 to 0.5 mm. The first proglottids tho broader than long are not very short. These become successively longer, the last being longest. The increase in length, however, is not constant because short proglottids are to be found between long ones. Nor is the breadth of the strobila constant. Some proglottids are about quadrate while others are 2-3-4 times longer than broad. Proglottid limits are poorly defined rendering the strobilation indistinct. The angles of the proglottids are not



prominent hence the worm has the appearance of a continuous ribbon. The description thus far is based on the original description as given by Parona (1898:8-9). In the toto preparations which the writer has studied there were a few mature proglottids one of which is delineated (Fig. 108). The uterus of this proglottid contained a few eggs but these have been omitted in the drawing. This segment measured 1.7 mm. long by 0.9 mm. broad. It was thin and flat but considerably thicker than proglottids of an equal state of development from *O. perspicua* or *O. natterer*.

A genital pore is situated near the middle of the margin of each proglottid. It alternates irregularly from left to right. There is no genital papilla nor is the pore marked by a deep depression as is sometimes the case in *O. grandis*. The vagina and cirrus-pouch open very near each other but in this toto preparation it was impossible to tell whether there was a common genital sinus. If present at all it was very shallow. The other drawings (Figs. 106, 107) do not show such a structure.

Testes (Fig. 108) are 100-108 in number. Their dimensions are 0.063 by 0.027 mm. to 0.080 by 0.027 mm., the long axis being perpendicular to the long axis of the worm. They are arranged in narrow bands situated well away from the vitellaria. In this respect the species resembles *O. calmettei*. None of the testes are posterior to the ovaries though Parona's drawing which has been reproduced (Fig. 193) for purposes of comparison shows them there. The vas deferens (Fig. 108) forms a small mass of coils in the mid-region of the proglottid. Within the cirrus-pouch is the much coiled ductus ejaculatorius (Fig. 107). The ductus passes over into the thicker-walled and more muscular cirrus. When under certain conditions the cirrus is protruded the greater part of the ductus ejaculatorius is crowded out into the dilated basal part of the cirrus (Figs. 106, 107). In this condition the cirrus is very similar to that described and figured by Schwarz (1908) for *O. marenzelleri*. He, however, claimed that the whole cirrus-pouch was evaginated. In this he misinterpreted the facts for only the cirrus and a part of the ductus are pushed out. Schwarz's drawing (reproduced Fig. 199) shows the cirrus-pouch in its normal position. In *O. marenzelleri* the distal half of the evaginated cirrus is filiform. This condition has not been seen in the present species yet it seems highly probable that a part of the coils of the ductus can be pushed through the basal part of the cirrus and thus form a filiform cirrus. Unless this be the case it is difficult to understand how copulation can be possible. The large number of coils of ductus ejaculatorius in this species furnishes a differentiating character between this species and *O. marenzelleri*. The

cirrus-pouch (Fig. 107) is large and very muscular. Its length varies from 0.27 to 0.34 mm. Its breadth is about 0.136 mm. and its length, according to Parona, is 0.33 mm. The ratio of the length of the cirrus-pouch to the breadth of proglottid is 1:4 or 2:5.

The vagina lies either anterior or posterior to the cirrus-pouch, but it does not cross the latter. Its course after reaching the median field is frequently quite sinuous. Near its opening (Figs. 106, 107) it has a very heavy sphincter muscle. In some parts of the vagina its lumen is narrow while in other regions it may be widely dilated. The lobes of the ovary are flattened. They are more elongate and narrower than in *O. marenzelleri*. The paired vitelline ducts cross the ovary on the ventral side. The uterus in mature proglottids is a median tube extending the length of the proglottid. No ripe proglottids could be examined so the number of lateral uterine out-pocketings could not be accurately determined. The drawing, however, (Fig. 108) indicates that probably about 20-30 lateral pouches would be developed on either side. No ripe eggs were present in the material examined.

The description and drawing of the mature proglottid shows this to be a species which falls readily into the group of Proteocephalids infesting snakes. The writer's description and drawings do not agree very well with Parona's except as to size, position of genital pore and length and shape of cirrus-pouch. From his drawings which have been reproduced (Figs. 192, 193) it appears that he has confused certain organs. The lower portion of the uterus in his drawing is undoubtedly the bilobed ovary. The position of the testes posterior to the ovary in his figure cannot be explained except on the supposition that he mistook parts of the organs of the interovarial space for testes. The sinuous duct which he shows as the vas deferens extending back from the cirrus-pouch to the ovary is not the vas deferens but the vagina which in fact passes below the coils of vas deferens before reaching the middle of the proglottid. The mass of coils of the vas deferens is poorly shown at the inner end of the cirrus-pouch. The opening of the vagina, the vaginal sphincter and the first part of vagina along the length of the cirrus-pouch he has omitted altogether or he has confused these with a part of the cirrus-pouch. The cirrus-pouch as he drew it seems to be made up of lamellae. In a poor preparation the cirrus-pouch might have had this appearance. The cirrus within the cirrus-pouch is not properly delineated. The uterus in an early stage may possibly have had the single anterior lateral pouch on either side as he has shown it. The writer has not seen a proglottid as nearly ripe as this one was and so is not able to judge as to the actual structure of the uterus. The testes and vitellaria he (Parona) has omitted from his drawings. It

seems highly probable that Parona's drawings are intended to represent the same species as do the writer's. The apparent difference probably came about through Parona's using poor preparations for study.

*O. trimeresuri* (Parona) in size is much smaller than *O. grandis*, *O. marenzelleri* and *Crepidobothrium gerrardii*. Moreover in number and arrangement of testes, size and proportions of cirrus-pouch and cirrus these three species differ greatly from *O. trimeresuri*. In size this species is more nearly related to *O. calmettei* but in the latter species the relations of the cirrus, cirrus-pouch and vagina are different. The testes in *O. trimeresuri* are arranged much as they are in *O. calmettei* but the size of the head and the suckers differ greatly. *O. nattereri* and *O. perspicua* are smaller, more delicate and have very different relations of cirrus, cirrus-pouch, vagina, and testes. This form differs from any other species thus far described from snakes yet it has its closest affinities with *O. calmettei*, likewise parasitic in one of the Crotalinae:

#### OPHIOTAENIA CALMETTEI (Barrois)

[Figs. 11, 109, 110, 155, 156, 197, 198]

1898:	<i>Ichthyotaenia calmettei</i>	Barrois	1898:1-3
1898:	<i>Ichthyotaenia raillieti</i>	Marotel	1898:99-101
1898:	<i>Ichthyotaenia calmettei</i>	Lühe	1898:652
1899:	<i>Ichthyotaenia calmettei</i>	Marotel	1899:34-42
1901:	<i>Ichthyotaenia racemosa</i>	Parona	1901:3
1908:	<i>Ichthyotaenia calmettei</i>	Schwarz	1908:24-26
1911:	<i>Ophiotaenia calmettei</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Observed length 27-40, and even up to 80 cm. Maximum breadth 0.97-1.2-2.0 mm. Proglottids numerous, first broader than long, subsequent ones quadrate or even much longer than broad. Mature proglottids about 0.85 mm. square. Ripe proglottids 2-3-4 mm. long by 1.0-1.2 mm. broad. Strobilation not clear. Scolex spheroidal or tetragonal, without rostellum, without hooks, without fifth sucker. Anterior face of same flattened, with small elevation at center. Head 1.0-1.3 mm. broad, 0.60 mm. long, 0.935 mm. thick. Suckers four, somewhat globular, with deep cavity. Diameter of sucker opening 0.12-0.17-0.185 mm. Diameter of sucker 0.27-0.300-0.408 mm. Neck 0.580-0.980 mm. broad by 4-5-8 mm. long.

Genital organs typical of genus. Genital aperture irregularly alternating. Situated at or near middle of proglottid margin. Genital sinus



shallow. Vagina anterior or posterior to cirrus-pouch. Vaginal opening frequently dorsal to cirrus-pouch. Testes 130-160 in number, arranged in two lateral fields. Size of testes 0.026-0.04-0.06 by 0.053-0.07 mm. Vas deferens a mass of coils extending from cirrus-pouch to mid-field. Cirrus-pouch 0.25-0.29-0.33 mm. long by 0.100-0.136 mm. broad. Ratio of length of cirrus to proglottid breadth 1:6-1:5 in mature and 1:4 in ripe proglottids. Ductus ejaculatorius with numerous coils. Cirrus broad, muscular, not seen protruded.

Vagina broad at distal end, never crossing cirrus-pouch in course to mid-field. Course of vagina to interovarial space sinuous. Sphincter vaginae present. Receptaculum seminis not seen. Ovarian lobes slender in young proglottids, broad in old. Vitellaria with small follicles. Uterus when fully developed possessing 24-35 lateral pouches on either side. Uterine pores ventral, 2-4-5 in number. Eggs provided with three membranes. Outer membrane variable in size, second one thicker, 0.022-0.024 mm. in diameter, inner one granular, irregular, 0.014 mm., embryo 0.012 mm.

Habitat: In intestine of *Lachesis (Bothrops) lanceolatus* L.

Host	Locality	Collector	Authority
<i>Lachesis (Bothrops) lanceolatus</i> L.	Martinique	Calmette	Barrois
<i>Lachesis (Bothrops) lanceolatus</i> L.	Martinique	Guérin	Marotel
<i>Lachesis (Bothrops) lanceolatus</i> L.	São Paulo, Brazil	Adolf Lutz	La Rue (the present paper)

Barrois' (1898) description of this species while meager and unaccompanied by drawings agrees fairly well with the descriptions of later investigators. His specimens came from *Lachesis (Bothrops) lanceolatus* L. from Martinique from which host they were secured by Professor Calmette. Later in the same year Marotel (1898) briefly described this species under the name *I. raillieti*. His specimens came from *Lachesis (Bothrops) lanceolatus* L. from Martinique. Lühe (1898) called attention to the fact that *I. raillieti* was a synonym of *I. calmettei*, and he included the form in his list of species of Ichthyotaenia. Marotel (1899:34-42) in a more extended paper described this species. His paper is accompanied by several drawings.

Parona (1901) listed this species in a record of parasites from South America under the name of *Ichthyotaenia racemosa*. His specimens are from *B. lanceolatus* L. from São Paulo, Brazil. Schwarz (1908:24-26) added but little to the work of Barrois and Marotel. He

determined that there was no rostellum. La Rue (1911:481) included this form in a list of species of *Ophiotaenia*.

This study is based on material which Professor H. B. Ward secured for the writer's study from Professor Parona. Professor Parona's material bore the label, "*T. (Oöchoristica) racemosa* S. Paulo, racc. A. Lutz." This is evidently the material on which Parona (1901) based his report. There he stated that it came from *Bothrops lanceolatus* L. The material consisted of seven or eight pieces to one of which a head was attached. The head was cleared in glycerine and studied in that condition while some of the smaller pieces were stained and mounted as toto preparations. The identification of the material was made from these preparations. The report is also based upon data secured from the papers of Barrois (1898), Marotel (1899), and Schwarz (1908).

The longest piece which the writer observed measured 270 mm. long by 2.0 mm. broad. Barrois (1898) states that he observed a length of 35-80 cm. by a breadth of 0.97 mm. for this species. Marotel's (1899) specimens measured up to 35-40 cm. long by a maximum breadth of 1.2 mm. Schwarz (1908) reported a breadth of 1.5 mm. The strobila is made up of many proglottids, according to Barrois as many as 289. The proglottids are closely joined to one another. As a rule no inter-segmental furrows can be seen with the unaided eye. In a single piece the strobila was strongly contracted and here the strobilation was evident. The surface of many of the proglottids is thrown into numerous longitudinal folds.

The scolex is club-shaped according to Barrois and Marotel, spherical according to Schwarz. The figures of the head as delineated by Marotel and Schwarz are reproduced (Figs. 155, 156). Barrois and Schwarz reported that there was no fifth sucker and no rostellum while Marotel thought that the slight elevation at the middle of the head (Fig. 156) was a rudimentary rostellum. He saw no fifth sucker. Marotel states that the globular suckers are directed anteriorly. The head (Fig. 11) which the writer observed was cleared in glycerine. It presents a somewhat tetragonal face with a small elevation at its center which is not a rostellum and upon which there is no fifth sucker. The suckers are placed in the corners of the anterior face and they are directed anteriorly. Slight grooves or wrinkles which do not extend to the apex partially divide the head into quadrants. The suckers are nearly round in outline and they lack any trace of the inturned lower margin which is a characteristic of the suckers of *Crepidobothrium gerrardii*. Suckers measure 0.39-0.408 mm. in diameter while the openings of the suckers measure 0.17-0.185 mm. in diameter. The sucker

cavity is deep. This head is 1.19 mm. broad, 0.60 mm. long, 0.935 mm. thick. The comparative table which follows presents the data on the head as secured by Barrois, Marotel, Schwarz, and the writer.

Head		Suckers		Diameter of sucker opening	Authority
Shape	Size	Shape	Diameter		
Club-shaped	breadth 1-1.3 mm.	.....	0.32-0.34 mm.	.....	Barrois (1898:2)
Club-shaped	breadth 1.05 mm.	globular	0.27-0.30 mm.	0.120 mm.	Marotel (1899:36)
Spheroidal	breadth 1.0 mm.	.....	0.30-0.34 mm.	0.120 mm.	Schwarz (1908:24)
Somewhat tetragonal	breadth 1.19 mm. length 0.60 mm. thickness 0.935 mm.	round in outline	0.39-0.408 mm.	0.17-0.185 mm.	La Rue (the present paper)

The neck of the specimen observed by the writer measured about 5-8 mm. long by 0.980 mm. broad. Its limits could not readily be determined in a glycerine preparation. Marotel states that the neck is 4 or 5 mm. long and 0.580 mm. broad at its narrowest place. Barrois and Schwarz do not state its dimensions. The first proglottids are much broader than long. These increase in length more rapidly than in breadth. Marotel (1899) states that at 20 mm. from the head the proglottids measure 0.255 mm. long by 0.63 mm. broad; at 25 mm. 0.65 by 0.65 mm. i. e., they are quadrate; at 30 mm., 0.71 mm. long, 0.67 mm. broad; at 40 mm., 1.45 by 0.75 mm., and the last proglottids are 3 to 4 mm. long by 1.0 mm. broad. In material examined by the writer nearly mature proglottids measure as much as 0.9 mm. broad by 0.55 mm. long and mature proglottids about 0.85 mm. square or some of them may be a little longer than broad. Ripe proglottids measure 2-3 mm. long by 1.0-1.2 mm. in breadth. In some contracted regions of the strobila the breadth may measure as much as 2.0 mm.

The sexual aperture is irregularly alternating, situated in mature proglottids at or slightly anterior to the middle of the margin. In ripe proglottids it may be either anterior or posterior to the middle. Both cirrus and vagina open into a common genital sinus which is very shallow. The vagina lies anterior or posterior to the cirrus-pouch with almost equal frequency. In ripe proglottids frequently and in mature proglottids more rarely, the vagina may open dorsal to the cirrus-pouch.

The testes (Figs. 109, 110) number from 130 to 160 in the writer's preparation and these numbers are also about the limits observed by the other investigators. They measure from 0.026 to 0.037 mm. by 0.053 to 0.063 mm. in the writer's preparations. Others report them as measur-



ing 0.06 by 0.04 mm., 0.062-0.072 mm., and 0.07 by 0.04 mm. They are arranged in two fields which in elongated proglottids are near the ventral excretory vessels while in contracted proglottids (Figs. 109, 110) they are some distance from the ventral vessels. In the former case the testes of each field are arranged in two irregular rows while in the latter case the testes of each field are irregularly arranged in a broad zone. The testes are dorsal to the uterus. The vas deferens forms a mass of coils which extend from the cirrus-sheath nearly to the middle of the proglottid. The writer's drawings (Figs. 109, 110) show it more heavily developed than do the figures of Marotel (1899) which are reproduced (Figs. 197, 198).

The cirrus-pouch is relatively short and broad, 0.25-0.29 mm. long by 0.100-0.136 mm. broad. In the broad mature and ripe proglottids it extends but a short distance within the vitellaria. The ratio of its length to the breadth in mature proglottids is about 1:6, in ripe proglottids about 1:5 or 1:5.5, in the ripest proglottid observed about 1:4. Schwarz states that the cirrus-pouch is about 0.33 mm. long. The ductus ejaculatorius (Fig. 109) has numerous coils. The unprotruded cirrus is broad and muscular. The writer has not seen it protruded and no other investigator reports having seen it thus. An examination of Marotel's figures which have been reproduced (Figs. 197, 198) shows fewer coils of ductus ejaculatorius and of vas deferens than do the drawings of the writer (Figs. 109, 110). This can be explained by the assumption that Marotel could not follow these structures out completely in his preparation which he states was made from material in a poor state of preservation. The material upon which the writer worked was in a fair state of preservation and in preparations made from it these ducts could be traced with ease.

The vagina at its distal end is broad, measuring 0.09-0.12 mm., a breadth due in part to the breadth of its lumen and in part to the thickness of its sphincter vaginae. In this region the vagina is nearly as broad as is the cirrus in its basal portion. In its course to the middle of the proglottid the vagina never crosses the cirrus-pouch. Arrived at the middle of the segment it bends sharply and takes a sinuous course posteriad to the interovarial space which it enters after passing over the dorsal side of the ovary, not the ventral as Marotel figures it. There are no coils of the vagina anterior to the ovary. A receptaculum seminis has not been observed tho from its occurrence in other species in the genus its presence in this species may be inferred. The lobes of the ovary in nearly mature proglottids are more slender and more pointed at the extremities than in mature and ripe proglottids. In well

elongated segments the lobes of the ovary assume the form figured by Marotel (Figs. 197, 198).

The vitellaria are lateral, and made up of small follicles. The vitelline ducts cross the ventral surface of the ovary instead of lying some distance anterior to it as Marotel figured them. In mature proglottids the uterus is a median tube. The early development of the lateral pouches (Figs. 110, 198) may be traced as small somewhat excentric bulbous enlargements of the median tube. This is not essentially different from *O. filaroides* and *O. perspicua*. These enlargements may attain some size before any uterine eggs appear. In early stages there is considerable resemblance to the condition shown in Marotel's figure (reproduced Fig. 198) of the ovigerous segment of *O. calmettei*. Later, however, many of these pouches (Fig. 109) extend toward the sides and the uterus resembles that of other species of the genus. The walls of these pouches are not very easily observed so Marotel may have overlooked them in his specimens. The pouches number 24-35 on either side. Two to four or five ventral uterine pores were observed in some of the riper proglottids. The uterine eggs in the alcoholic material are surrounded by three membranes. The outermost very thin hyaline membrane measures from 0.024 to 0.026 mm. The second, a thick and homogeneous membrane, measures 0.022 mm. The inner membrane is thick, granular and more or less irregular in outline. It measures 0.014 mm. while the six-hooked embryo measures 0.012 mm. in diameter. Marotel (1899) states that the eggs are globular, with two membranes, the outermost one being thin and membranous, 0.065 mm. in diameter, and the other, a homogeneous and somewhat thick membrane, 0.024 mm. in diameter. This membrane corresponds in size and description to the one which the writer calls the middle membrane. He further states that the embryo is granular but does not give its dimensions.

This species varies from the *O. racemosa* described by Schwarz (1908) in the much larger size of the head, the larger size of the suckers, and the relative prominence of the same. The number and arrangement of the testes are radically different. In the length of the cirrus-pouch, in the number of coils of ductus ejaculatorius they differ greatly. In the size of the distal end of the vagina there is considerable difference. The character of the diverticula of the uterus is not the same. In this species the uterus extends back to the ovary while in *O. racemosa* as described by Schwarz it does not. The vitellaria are much alike in character. This species is much smaller than *O. grandis*. The heads are of about the same size but not alike in shape. The relations of cirrus, cirrus-pouch and vagina are different. There is a wide differ-

ence in the number of testes and in the number of uterine outpocketings. The hosts and geographical distribution are also widely different.

It varies from *O. marenzelleri* in having a much smaller head, smaller suckers and in the lesser prominence of the same, in its smaller proglottids and in its smaller number of testes. The relations of the cirrus and cirrus-sheath are quite different. The fact that the vagina lies usually posterior to the cirrus-pouch in *O. marenzelleri* constitutes a marked difference. The shape of the ovaries is somewhat different. In *O. marenzelleri* the marked bending of the vagina in its course to the middle of the proglottid is very unlike the condition in this species. *O. calmettei* is larger than *O. trimeresuri*. It has a larger head, larger suckers and more than twice as many testes. The relations of the unprotruded cirrus and the cirrus-pouch are much alike in the two species. *O. calmettei* is so much larger than *O. perspicua*, *O. nattereri* or *O. pigmentata* that any possibility of confusion with them is precluded. It is likewise much larger than *O. filaroides* and *O. lönnbergii* which occur in amphibians. *O. calmettei* most nearly resembles *O. grandis*, *O. marenzelleri* and *O. trimeresuri* which likewise occur in the Crotalinae.

#### OPHIOTAENIA PUNICA (Cholodkovski)

[Figs. 153, 187, 188]

1908: <i>Taenia punica</i>	Cholodkovski	1908:418-20
1910: <i>Proteocephalus punicus</i>	Hall	1910:148
1911: <i>Ophiotaenia punica</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Length as much as 10 cm. Breadth up to 2.75 mm. Head large, 1.5 mm. broad, unarmed, somewhat tetragonal in shape. Suckers four, large, round, 0.7 mm. in maximum diameter. Sucker musculature heavier on inner half. Neck short. Segmentation not evident. Proglottids attached by full width. First proglottids broader than long, older ones quadrate and finally longer than broad. The genital opening alternates irregularly, is situated near middle of proglottid margin. Testes very numerous, about 200, situated in two well defined lateral fields. Cirrus-pouch slender, extending  $\frac{1}{4}$  to  $\frac{1}{3}$  across the breadth of the proglottid. Lobes of ovary long, slender, rough in outline, connected by a long slender mid-piece. Vitellaria lateral, composed of small follicles. Uterus median. Eggs not observed.

Cholodkovski (1908:418-420) reported this species from a dog in Tunis (Island of Dscherba). Since this is a peculiar host in which to



find a species normally occurring in a lower vertebrate his description is here quoted omitting only the first and last paragraphs:

"Nicht ohne Überraschung habe ich also in einer mir von Dr. M. Weinberg zugesandten Tänie aus dem Darne eines Hundes eine neue Species erkannt, die ich hier in aller Kürze beschreiben will. Das Material (in Formol aufbewahrt) stammte aus Tunis (Insel Dscherba) und bestand aus drei unvollständigen Strobilae, deren grösste eine Länge von etwa 10 cm erreichte. Der Scolex ist sehr gross (1.5 mm breit), unbewaffnet, mit vier starken rundlichen Saugnäpfen und einer kleinen Erhöhung auf dem Scheitel versehen. Die Saugnäpfe sind etwas asymmetrisch gebaut, indem ihre innere Hälfte merklich dicker als die äussere ist; der grösste (äussere) Durchmesser derselben beträgt 0.7 mm. Gleich hinter einem sehr kurzen Halse wird die Strobila etwa 2 mm., dann bis 2.75 mm. breit, nach hinten aber allmählich etwas enger. Eine äussere Gliederung ist auf ganzen Stücken unbemerkbar und lässt sich erst auf gefärbten Balsam—oder Glycerinpräparaten in der Gestalt von sehr schwach ausgesprochenen Querrinnen konstatieren. Die ersten Proglottiden sind breiter als lang, (vide Fig. 188 which is reproduced from Cholodkovski's figure 3) dann werden sie allmählich länger, quadratisch und endlich länger als breit; in keinem der mir vorgelegenen Exemplare waren aber ganz reife; d. h. fertige Eier enthaltende Proglottiden vorhanden. Die Geschlechtsöffnungen alternieren unregelmässig. Die stark in der Querrichtung verlangerten Ovarien liegen dicht an der hinteren Grenze der Proglottis, der Dotterstock ist sehr klein, der Uterus bildet einen geraden, in der Mittellinie der Proglottis nach vorn verlaufenden Stamm. In völlig reifen Proglottiden treibt er vielleicht auch laterale Zweige, in meinen Exemplaren war er aber immer einfach (vide Fig. 187 reproduced from Cholodkovski's figure 4). Die zahlreichen Hoden liegen in zwei lateralen Längsfeldern nach innen von den grossen Excretionsgefässen. An der Stelle letzteren befindet sich in totalen, mit Boraxkarmin tingierten Präparaten der reifsten mir vorgelegenen Proglottiden eine körnige Masse, deren Bedeutung mir unklar geblieben ist, da ich aus Mangel an Material keine darauf bezüglichen Schnittserien verfertigen konnte.

"Da die hier beschriebene Tänie allem Anschein nach eine neue Species darstellt, so schlage ich vor, sie nach ihrem Fundorte *Taenia punica* zu nennen."

This species was overlooked by the writer until his attention was called to it by Hall's article (Hall 1910) in which it is stated that the species belongs to the genus *Proteocephalus*. The paragraphs (Hall 1910:146 and 148) in which he gives his reasons for this belief are here quoted:

"In compiling a key to the dog tapeworms, an examination of Kholodkovski's (1908) description and figures of *Taenia punica* from the dog showed that the cestode in question probably belongs in the genus *Proteocephalus* Weinland. The head, the uterine stem, the position of the ovaries at right angles to the uterine stem, and the position of the testes and the genital canals all indicate this. The granular strand of uncertain nature which Kholodkovski noted in the position of

the excretory canals can hardly be anything other than the vitellaria, in the location usual for the species of the genus *Proteocephalus*. Kholodkovski states that the vitellarium is very small, but it seems likely that he has mistaken something else for the vitellarium. A comparison of the figures with mounted specimens of the worms of the genus *Proteocephalus* leaves no reasonable doubt on this point, and it is the opinion of the writer and Dr. B. H. Ransom, with whom the point was discussed, that it is more likely that the dog from which the tapeworms were obtained had just eaten the true host, some fish, reptile, or batrachian, than that the dog was the true host by virtue of a normal, even though unusual, infection with larval form. Fuhrmann appears to have overlooked the unusual features of this worm in his review of Kholodkovski (1909), and states that the anatomy is that of species of *Taenia*."

"*Taenia punica* Kholodkovski, 1908, should therefore be known as *Proteocephalus punicus* (Kholodkovski, 1908) Hall, 1910, a combination proposed here for the first time . . . . ."

La Rue (1911:481) included this species in the genus *Ophiotaenia*.

After making a careful study of Cholodkovski's description and drawings, and after comparing them with many specimens of Proteocephalidae the writer agrees with Hall that the normal host of this species is not the dog. In the writer's opinion the true host is a snake. This cestode having its testes in two fields does not resemble any of the species of *Proteocephalus* thus far described from fish. The *Proteocephalids* that infest the lizards belong to the genus *Acanthotaenia* and these are distinguished from other *Proteocephalids* by the presence of spines on the head and neck. The *Proteocephalids* thus far described from Amphibia are small with rather small heads. Their genital organs, however, resemble those of *Taenia punica*. It is also true that in this respect they agree with the *Proteocephalids* of snakes. The species from snakes vary in size from small to large. Some of the species have large heads with large and prominent suckers. Their genital organs much resemble those of *Taenia punica*. As in the latter species the vitellaria of the *Proteocephalids* of snakes are sometimes composed of small follicles which refuse to take the stain well. In such cases it is easy to overlook the vitellaria. As an instance of this might be mentioned the *Taenia eunectes* A. J. Smith in which the coils of the ducts in the interovarial space were thought to be the vitellaria. For these reasons and also on account of the size of the head and strobila the writer suggests that the true host of *Taenia punica* is a snake, and that *Taenia punica* belongs to the genus *Ophiotaenia* and should therefore be known under the name *Ophiotaenia punica* (Cholodkovski, 1908) La Rue.

## OPHIOTAENIA MARENZELLERI (Barrois)

[Figs. 37, 199]

1898:	<i>Ichthyotaenia marenzelleri</i>	Barrois	1898:2-3
1908:	<i>Ichthyotaenia marenzelleri</i>	Schwarz	1908:26-27
1911:	<i>Ophiotaenia marenzelleri</i>	La Rue	1911:481

Specific Diagnosis: Characters of genus. Observed length of strobila as much as 40 cm. Maximum breadth 1.5-2.0 mm. Scolex large, round, muscular, 1.2-2.0 mm. broad, well set off from neck. No rostellum. No hooks. No functional fifth sucker. Suckers four, 0.60-0.70 mm. in diameter. Neck not observed. Strobilation distinct. Proglottids closely attached. Length of proglottids as much as 5.5 mm., maximum breadth of same 1.5-2.0 mm. Excretory system composed of two pairs of lateral vessels. Genital organs as in genus. Genital aperture marginal, irregularly alternating, situated near middle of lateral margin of proglottid. Testes numbering 150-200-240, measuring 0.06-0.07 mm. in diameter, situated in two lateral fields. Cirrus-pouch large, extending about one-third across the proglottid breadth. Cirrus, when protruded, swollen at base and filiform at tip, 1 mm. long. Vagina usually posterior to cirrus-pouch. Uterus when completely developed possessing 20-25 lateral outpocketings on either side. Eggs provided with two membranes. Diameter not known.

Habitat: In intestine of *Ancistrodon piscivorous* Holbr., southern United States.

Barrois (1898) in a very brief description, unaccompanied by drawings, proposed this species. Schwarz (1908:26-27) redescribed this species using Barrois's material. His description was accompanied by three drawings. La Rue (1911:481) included this species in the new genus *Ophiotaenia*.

The material which Barrois and Schwarz had for study was collected by Doctor Calmette, Dec. 22, 1897, from *Ancistrodon piscivorous* Holbr., a snake indigenous to the southern United States. Unfortunately specimens of this species could not be had by the writer for study hence the data used in the following description are derived only from the articles of Barrois (1898) and Schwarz (1908). A study of



new material is desirable in order that a more complete knowledge of this form may be had.

This is one of the largest of the species of *Ophiotaenia*. The observed length is about 40 cm. Schwarz (1908:26) thought that perhaps the length might exceed that of *O. calmettei* (35-80 cm.). The maximum breadth observed was 1.2-2.0 mm. The scolex is large, round and muscular. It has a breadth of 1.5-2.0 mm. Barrois described an unarmed rostellum. Schwarz found no rostellum, nor does his delineation of the head, which is reproduced (Fig. 37), show such a structure. The scolex is clearly set off from the neck. The four suckers are muscular, prominent and nearly circular. They measure 0.60-0.70 mm. No functional fifth sucker is present. The neck was not described by Barrois or by Schwarz. The strobilation is distinct, altho the strobila has no indentations. Proglottids are strongly attached. The length of the largest proglottids is about 5.5 mm. and the maximum breadth about 1.5-2.0 mm. The excretory system is made up of two pairs of lateral vessels, a dorsal and a ventral.

The genital aperture is marginal and it alternates irregularly. It is situated about the middle of the proglottid. The testes (Fig. 199) lie in two well marked lateral fields between the vitellaria and the uterus. Barrois gives 230-240 as their number, Schwarz 150-200. They measure 0.060-0.070 mm. Of the cirrus-sheath and vas deferens Schwarz says "the relation of the cirrus-sheath and vas deferens is especially characteristic for this form. In ripe segments the greater part of the cirrus-sheath is completely evaginated. There seems to exist a special muscular apparatus which withdraws the cirrus-sheath, when completely sexually mature, from the proglottid, so that it projects free from the margin. In young segments it lies in its normal position within the segment".

Schwarz has evidently misinterpreted the appearance in this case. His own drawings show no evagination of the cirrus-pouch but a complete evagination of the cirrus which is thick at the base, and filiform at the tip. From this heavy base the ductus ejaculatorius runs straight through the now greatly shrunken cirrus-pouch. There are some coils of the ductus ejaculatorius within the basal part of the cirrus itself. The writer has observed this condition in *O. trimeresuri*. Schwarz states that the cirrus is about 1 mm. long in *O. marenzelleri*. In his drawing the cirrus-pouch extends about  $\frac{1}{3}$  across the proglottid breadth. The vas deferens forms a mass of coils before entering the cirrus-pouch.

The vagina opens usually posterior to the cirrus-sheath. Its course to the middle of the proglottid forms an arc. At the middle of the proglottid it bends sharply posteriad and then its course is direct to

the interovarial space. The uterus is a median tube from which arise on either side many lateral pouches; 20-25 are figured in Schwarz's drawing. The ovary is relatively large and its lobes are somewhat wing-like in shape. The eggs are provided with two membranes. No processes arise from the outer one. No measurements of the eggs were given by Barrois or Schwarz.

The species is clearly differentiated from the other large species of the genus by the size and shape of the head and suckers. The relations of the cirrus and cirrus-pouch vary greatly from the plan common to the other large species of the genus. *O. trimeresuri* which has the same relations of cirrus and cirrus-pouch is considerably smaller. *O. grandis* resembles it in having the same host species and in being of large size. *O. grandis* has, however, a very much smaller head which is not readily distinguished from the strobila. It has much smaller suckers and greatly different relations of cirrus and cirrus-pouch. Its cirrus is short and thick. It also has very many more uterine outpocketings. *O. marenzelleri* is not to be mistaken for *O. racemosa*, *O. nattereri*, *O. pigmentata*, or *O. perspicua* on account of its much larger size. *O. filaroides* and *O. lönnbergii* being from Amphibia and also being much smaller cannot be confused with *O. marenzelleri*.

#### OPHIOTAENIA GRANDIS La Rue

[Figs. 38, 97-101]

1911: *Ophiotaenia grandis* La Rue 1911:481

Specific Diagnosis: Characters of genus. Body very long (fragments 200 mm.) by 2.75-4.25 mm. broad in region of ripe proglottids. Neck 5-8 mm. long. First proglottids much broader than long; proglottids with developing sexual organs quadrate or nearly so; ripe proglottids quadrate or much longer than broad. Head large, 1.0-1.2 mm. broad at base of suckers. No fifth sucker or rostellum, no hooks. Suckers nearly circular, deep and muscular, measuring about 0.34 by 0.36 mm. Genital aperture marginal, irregularly alternating, situated near middle of proglottid. No genital papilla but sometimes a deep depression about genital pore. Testes large, numerous, 200-250 in number, arranged in two broad lateral fields. Cirrus-pouch 0.24-0.26 mm. broad, 0.64-0.75 mm. long, length equal to  $\frac{1}{3}$ - $\frac{1}{5}$  of proglottid width. Cirrus short and heavy. Few or no coils of ductus ejaculatorius in cirrus-pouch. Vagina anterior or posterior to cirrus-pouch. Sphincter vaginae heavy. Uterus with 40-60 lateral outpocketings on either side.

Ventral uterine openings 2-8 in number. Outer egg membrane ellipsoidal, 0.026 by 0.037 mm. or sometimes spherical 0.032 mm. in diameter; second egg membrane 0.021-0.023 mm. Embryos 0.015-0.016 mm. Outer membrane smooth.

Type: Specimens in collections of United States Bureau of Animal Industry, No. 14854.

Habitat: In intestine of *Ancistrodon piscivorus* Holbr. (type host), National Zoological Park. The locality from which this host came is not known. The species is found only in North America.

La Rue (1911:481) described this species in a preliminary way. Six or eight heads together with numerous pieces in a bottle bearing the U. S. Bureau of Animal Industry number 14854 were labelled "*Ichthyotaenia*: host *Ancistrodon piscivorus*; location, intestine; locality Nat. Zoo. Park, collected S. S. Shawhan. Nov. 18, 1907." These were secured for the writer's study by Professor Ward.

No complete worm was found. The largest piece was 200 mm. long and 3.5 mm. broad at the anterior end and 4.25 mm. broad at the posterior end. This piece was made up of proglottids that were well advanced in development, being nearly mature at the anterior end and nearly ripe at the posterior end. The younger proglottids were not distinctly separated by furrows but the more mature ones showed very evident segmentation. Judging from the size of the segments and their state of development it seems likely that the whole worm would attain a length of 300-400 mm. or perhaps even more. Like other species of *Ophiotaenia* the body is quite flattened. However, the body is thicker than has been observed by the writer in *O. calmettei*, *O. nattereri*, *O. trimeresuri*, *O. perspicua*, and *Crepidobothrium gerrardii*. The head (Fig. 38) is large tho not so large as in *O. marenzelleri* (Barrois) or *Crepidobothrium gerrardii* (Baird). It measures 1.0-1.2 mm. in diameter at the base of the suckers. The scolex, measured from its tip to the base of the suckers has a length of 0.50-0.60 mm. There is no rostellum, no hooks, no fifth sucker, and from toto mounts no vestigial fifth sucker may be observed. As yet no sections of the head have been made.

The four deep suckers are borne on the broadest part of the head and these are directed outward. They are not prominent, are strongly muscular, nearly circular in outline and they lack the upward pointing projection that is always found in the suckers of *C. gerrardii*. The suckers measure 0.34-0.35 mm. in transverse axis by 0.35-0.36 mm. in longitudinal axis. The cavity of the sucker is deep. Its opening measures 0.15-0.17 mm. in longitudinal diameter by 0.20-0.22 mm. in transverse diameter. Immediately back of the head there is some-



times a large inflation (Fig. 38). Since this is not always present it must be due to the contraction of the heavy longitudinal muscles of the upper part of the neck. The neck itself is broad, thin and long, being 0.85-1.0 mm. broad by 4-8 mm. long.

The first proglottids are short, their breadth equalling several times the length. As the proglottids become older the shape changes from the rectangular to nearly quadrate or quadrate. Proglottids ranging in age from nearly mature to ripe are usually longer than broad. Those proglottids which show the beginnings of the cirrus-pouch and vagina measure 0.5 mm. long by 1.0 mm. broad while those in which the anlagen of the testes are appearing measure 0.680 mm. long by 0.850 mm. broad. Both length and breadth increase greatly as the segments near maturity. A few nearly ripe proglottids are broader than long, measuring 3.25 mm. long by 4.25 mm. broad. The longest proglottid found measured 8 mm. long by 2.75 mm. broad while many proglottids measure 3-5 mm. long by 2-3 mm. broad. The surface of the body is somewhat wrinkled, due perhaps to having lain twisted for a long time in the alcohol. There seem normally to be no furrows either longitudinal or transverse. Proglottid limits are not well defined in young proglottids but are well defined in the older ones.

The genital aperture is marginal, irregularly alternating. Frequently the aperture occurs on the same side in several successive proglottids but always in greater numbers on the left side. The greatest number of genital apertures found occurring successively on the left side was ten. No papilla marks the genital aperture. Indeed in many proglottids the muscles are so contracted about the genital aperture as to cause a deep depression (Fig. 100). In such cases it is noteworthy that the cirrus and vagina open to the exterior separately. In many cases it is doubtful if a true genital sinus exists. If present it is extremely shallow. The arrangement of the sexual organs agrees in general with that of other *Proteocephalids*.

The cirrus-pouch (Figs. 97, 98) is short and broad, and is broadest at the distal end. It is either straight or curved, depending upon the state of contraction of the proglottid and of the muscles in the region of the genital aperture. When the region of the genital aperture is depressed the cirrus-pouch is usually somewhat bent (Fig. 100). Its length is 0.64-0.75 mm. and its breadth 0.24-0.26 mm. The ratio of its length to the breadth of the proglottid is 1:3 or 1:5. The cirrus (Figs. 97, 98) when protruded is thick, short, straight and heavily muscled. It is continuous with the ductus ejaculatorius which forms no, or at least few, coils within the cirrus-pouch. The drawings (Figs. 97, 98) show only a slight twist or turn in this part of the ductus. This descrip-

tion and an examination of the figures makes it evident that the cirrus and cirrus-pouch of the present species are very different from the same organs in *O. marenzelleri* with which this species is closely allied. In that species there are many coils of the ductus ejaculatorius within the cirrus-pouch, and the cirrus when protruded is thick at the base but drawn out to a slender tip. Schwarz (1908) errs in saying that the cirrus-pouch is evaginated in *O. marenzelleri*. His own figures show the cirrus-pouch in situ. In the present species the vas deferens is thrown into numerous coils which serve as a vesicula seminalis. There are about 200-250 testes which are arranged in two lateral fields. The testes measure 0.04-0.05 mm. broad by 0.075-0.100-0.125 mm. long. The vagina opens to the exterior either anterior or posterior to the cirrus-pouch, with almost equal frequency. Out of 45 proglottids examined on this point the vagina in 21 cases opened anterior and in 24 cases posterior to the cirrus-pouch. A heavy sphincter vaginae 0.095 mm. long by 0.150 to 0.160 mm. broad, including vagina, surrounds the vagina near its opening to the exterior. The thickness of the sphincter alone is 0.040-0.070 mm. The vitellaria are follicular in structure, and lateral in position. Each follicle measures about 0.015 by 0.030-0.035 mm. A diagram (Fig. 99) made from a toto preparation shows that the arrangement of the organs of the interovarial space is similar to that figured for other Proteocephalids. The ovaries are thin dorsoventrally. The mid-piece connecting the ovarian lobes is slender and long. The uterus (Fig. 101) in maturing proglottids is a median ventral tube. From this are developed 40-60 lateral pouches on either side. These are formed by the method already described by La Rue (1909) for *O. filaroides*. No eggs are passed into the uterus until the outpocketings have attained a considerable size. Two or more preformed ventral uterine pores are developed before many eggs are present in the uterus. The largest number of the uterine pores in the material studied was eight. The eggs taken from the uterus of alcoholic specimens are usually ellipsoidal, measuring about 0.026 by 0.037 mm. over the outer membrane. Spherical eggs measure about 0.032 mm. The second membrane is spherical, 0.021-0.023 mm. in diameter. The third membrane closely invests the embryo which is 0.015-0.016 mm. in diameter. Mature eggs have smooth contours. There are no hooklets or holding organs on the egg membrane as Schwarz (1908) figures for the eggs of *O. nattereri* (Parona).

The present species differs from *O. marenzelleri* (Barrois) in having a smaller head, smaller suckers, larger proglottids, greater breadth, more numerous testes and more numerous uterine pouches. The character of the evaginated cirri of the two species is very different. It also

differs from *Crepidobothrium gerrardii* (Baird) in the size of the head and suckers, and in the character of the latter. *O. grandis* has a long unsegmented neck while *C. gerrardii* has almost no neck. *O. grandis* somewhat resembles *O. calmettei* in the size of the head and suckers. It differs from that species in the size of strobila and of proglottids, and in length of neck. *O. grandis* has a larger number of testes and a cirrus which differs greatly from that of *O. calmettei*. *O. grandis* is so much larger than *O. perspicua*, *O. nattereri* (Parona), *O. trimeresuri* (Parona), and *O. racemosa* (Rudolphi) that a possibility of confusing it with any of those species is precluded.

### CREPIDOBOTHRIMUM GERRARDII (Baird)

[Figs. 12, 13, 33, 34, 42, 111-115, 123, 124, 190, 196]

1850:	<i>Taenia racemosa</i>	Diesing	1850:511, in part
1860:	<i>Tetrabothrium gerrardii</i>	Baird	1860:446-448
1861:	<i>Tetrabothrium gerrardii</i>	Baird	1861:228-230
1864:	<i>Tetrabothrium gerrardii</i>	Diesing	1864:82
1898:	<i>Ichthyotaenia gerrardii</i>	Lühe	1898:652
1899:	<i>Crepidobothrium gerrardii</i>	Monticelli	1899:9-25
1899:	<i>Ichthyotaenia gerrardii</i>	Lühe	1899:525
1905:	<i>Taenia racemosa</i>	Shipley	1905:101
1908:	<i>Taenia eunectes</i>	Smith	1908:39-41
1911:	<i>Crepidobothrium gerrardii</i>	La Rue	1911:479-480

Specific Diagnosis: Characters of genus. Length of strobila as much as 45.6 cm. Maximum breadth 0.85-2.00 and even 6.0 mm. Strobila flat, thin and wrinkled. Proglottids closely attached. Segmentation indistinct. Head large, tetragonal, pyramidal, maximum breadth of same 0.935-1.3 or even as much as 1.75 mm., thickness a little less than breadth, length about 0.68-0.90 mm. Fifth sucker vestigial but with cavity open to exterior. Four suckers prominent, muscular, cordate, with lower margin interrupted and re-entrant into sucker cavity. Breadth of suckers 0.40-0.70 mm. Neck broad, not over 0.5-0.8 mm. long. First proglottids short, rapidly increasing in length. Mature proglottids quadrate. Ripe proglottids longer than broad. Length of same 1.7-2.3 mm. by 0.65-1.09 mm. broad.

Genital pore marginal, irregularly alternating, situated near middle of proglottid. Vagina anterior or posterior to cirrus-pouch. Opening of vagina dorsal to cirrus-pouch. Testes 200-400 in number, small, 0.035-0.050-0.080 mm. in diameter, situated in two lateral fields. Cirrus-



pouch 0.23-0.5 mm. long by 0.10-0.15 mm. broad. Length of same 4-5-6 times into the proglottid breadth. Several coils of ductus ejaculatorius in cirrus-sheath. Lumen of vagina large near opening. Sphincter vaginae heavy. Receptaculum seminis present. Ovary posterior, bilobed, lobes thick, short, irregular. Organs of interovarial space as in *Ophiotaenia*. Vitellaria small, loosely follicular, lateral. Fully developed uterus provided with 20-30 lateral pouches. Eggs possessing two (?) or three membranes. Outer membrane measuring 0.085-0.100 mm., second, 0.028-0.030 mm., embryo 0.016-0.018 mm. in diameter.

Habitat: In intestine of Boidae, a family of South American snakes.

Host	Locality	Collector	Authority
(?) <i>Ophiomorphus miliaris</i>	South America	.....	Diesing, 1850:511
<i>Eunectes murinus</i> (scytale)	South America	.....	Diesing, 1850:511
(?) <i>Bothrops jararacca</i>	South America	.....	Diesing, 1850:511
(?) <i>Ophis merremii</i>	Brazil	Natterer	Diesing, 1850:511
<i>Boa constrictor</i>	South America	Edward Gerrard	Baird, 1860:446-448
<i>Eunectes murinus</i> Wagl.	.....	.....	Shipley, 1905:101 (La Rue)
<i>Eunectes murinus</i>	.....	A. J. Smith	Smith, 1908:39-41 (La Rue)

In the discussion of the hosts of *Ophiotaenia racemosa* it was stated that *Ophiomorphus miliaris* and *Ophis merremii* were to be considered as probable hosts of that species. It is doubtful if they serve as the hosts of *Crepidobothrium gerrardii*. *Bothrops jararacca* is one of the Crotalinae and would not be likely to harbor *C. gerrardii*, but in all probability it would be the host of a species resembling *O. marenzelleri*, *O. grandis*, *O. trimeresuri*, and *O. calmettei*. These form a group quite distinct from the other *Ophiotaenia*. It is very likely that Diesing being unable to make a careful examination of the cestodes of these snakes grouped them all under the name *Taenia racemosa*. It is desirable to re-examine the specimens to which Diesing's description and notes refer, if they still exist. The hosts of *C. gerrardii* of which there is no doubt are *Eunectes murinus* Wagl. and *Boa constrictor* L.

This species was first reported by Diesing (1850:511) who called it *Taenia racemosa* Rud. His diagnosis agrees excellently with that of *Crepidobothrium gerrardii*. He includes as a host one of those species,

*Eunectes murinus* (*scytale*), from which this species has been reported several times. His description and habitat data are quoted in full:

"*Taenia racemosa* RUDOLPHI. *Caput* magnum tetragonum, acetabulis angularibus subterminalibus v. terminalibus, subovatis v. cordatis. *Collum* nullum. *Articuli* supremi brevissimi, subsequentes longiores et latiores, angulis rotundatis, ultimi longi parallelopiedi angustiores. *Penes* filiformes basi incrassati, marginales vage alterni. Longit. 2"  $1\frac{1}{2}$ "; latit. med. 1-3"; ultim. 1".

"*Taenia racemosa* Rudolphi: Synops. App. 692.—Dujardin: Hist. nat. des Helminth. 610.

"Habitaculum. *Ophiomorphus miliaris*, Martio.—*Eunectes Scytale*, Octobri, Febuario et Junio.—*Bothrops Mararacca* (misspelling for jararacca), Martio et Aprili.—*Ophis Merremii*, Januario, in Brasilia (*Natterer*): in intestin. M. C. V."

Baird (1860:446-448) described this species which was found by Mr. Edward Gerrard in the intestine of a *Boa constrictor* from South America. Since the name *Taenia racemosa* Rud. had already been applied to a different species of cestode the name suggested by Baird stands by reason of its priority. Baird's second description (1861:228-230) is a copy of the earlier description (1860:446-448). Because of the inaccessibility of either of these descriptions for many investigators the later diagnosis which alone was accessible is quoted:

" . . . . The species now to be described, however, was found by Mr. Edward Gerrard of the British Museum . . . in the intestine of a *Boa constrictor* from South America.

"The head is large, tetragonal; the four bothria disposed crosswise, joined by the margins; each of them large, round, and having on one side a strong ridge. Body depressed, narrow, articulated. No distinct neck. Anterior extremity of body very narrow, and the articulations there are extremely small, becoming larger as they descend, the inferior being quadrangular and rather large. The margins of the articulations somewhat annulated, but having no appearance of genital apertures. The head is about three-fourths of a line broad; but I could not discover any mouth. Apparently only fragments of these worms were obtained; but some of these detached pieces were about 18 inches in length.

"Hab. Intestines of *Boa constrictor*."

Diesing (1864:82) placed this species in the genus *Tetrabothrium* but with some reservation. His diagnosis is quoted in full in order that a comparison of it can be made with his diagnosis of *Taenia racemosa*, Diesing (1850:511):

"*Tetrabothrium Gerrardii* Baird. *Caput* magnum tetragonum, bothriis quatuor cruciatim oppositis subcircularibus magnis, marginalibus contiguis, singulo costa

.....<sup>1)</sup> Os.... Collum nullum. Corpus depressum augustum, articulis supremis angustissimis, posterioribus quadrangularibus. Aperturæ genitalium.... Longit. fragmenti 18", latit. capit.  $\frac{3}{4}$ "'.

"Habitaculum. *Boa Constrictor*: ex America meridionali, in intestinis (Gerrard)."

A comparison of the diagnosis just quoted and the earlier one by Diesing (1850:511) leaves no doubt that the two diagnoses concerned the same species, namely, *Crepidobothrium gerrardii*. Lühe (1898:652) included this species in a list of Ichthyotaenia from snakes. He gave no reason for considering it a member of this genus. Fuhrmann (1899:864) in a footnote made this statement concerning this species: "Lühe, M., *Oöchoristica* nov. gen. *Taeniadarum*. (Zoolog. Anz. 1898. No. 576) giebt an, dass *T. Gerrardii* (Baird) in das Genus *Ichthyotaenia* gehöre; dies ist aber wie mir Prof. Monticelli mitteilte und wie ich mich selbst an den von ihm nach den originalen angefertigten Zeichnungen überzeugen konnte, keineswegs der Fall. Es gehört diese Form in ein besonderes Genus, das Prof. Monticelli demnächst unter dem Namen *Crepidobothrium* publizieren wird." During the same year Monticelli (1899:9-25) made a report, accompanied by drawings, upon the type material of this species which was in the British Museum. He also studied some material which had been sent to him by Prof. Fr. Bell. As a result of this study he erected the genus *Crepidobothrium* for Baird's species alone. Lühe (1899:525) in a footnote discussed the position of this species which he still maintained belonged to the genus *Ichthyotaenia*. His ground for this belief was that the head and suckers which are different from those of other *Ichthyotaenia* constitute only a specific difference. He stated that the name *Crepibothrium* (Fuhrmann 1899) was a nomen nudum. He had not seen Monticelli's article and so was in no position to judge Monticelli's work.

Shiple (1905:101) made the following report of this species: "*Taenia racemosa* Rud. Diesing, Syst. Helm. I. p. 511. Many specimens from *Eunectes murinus* Wagl., it has also been described from the intestine of *Bothrops jararacca* Wagl." Thanks to Professor H. B. Ward who secured them for study, the writer has been able to examine some of Shipley's specimens from the host *Eunectes murinus*. They were probably from the same lot which Shipley recorded in the above quotation. They proved to belong to the species *Crepidobothrium gerrardii* (Baird). Smith (1908) found some cestodes in an anaconda, *Eunectes murinus*. He described them under the name *Taenia eunectes*.

<sup>1)</sup> "Each of them large, round and having on one side a strong ridge" Baird l. c." (Baird:1860 or 1861).



Upon request Doctor Smith sent some of this material to Professor Ward who has very kindly permitted the writer to study it. Study of this material has shown that it belongs to the species *Crepidobothrium gerrardii*. La Rue (1911:479-480) gave the synonymy of this species briefly and stated some of his findings.

A comparison of the diagnoses of Diesing (1850:511 and 1864:82) with the description by Baird (1861) and with the description by Monticelli (1899:9-25) leaves no ground for doubt that these investigators were reporting the same species. In certain respects the description by Smith (1908:39-41) differs radically from that of Monticelli. However an examination of Smith's material has shown that Smith made numerous misinterpretations which are the cause of the apparent discrepancies between his work and Monticelli's. In his study of this form the writer has found Monticelli correct in the main. It has already been stated that Shipley's material belonged to *C. gerrardii*.

The question concerning the correct name for this species must be settled. From a structural point of view this species cannot be retained in the genus *Taenia* nor in the genus *Tetrabothrium*. Anatomically this species is one of the Proteocephalidae. This has been recognized by Lühe (1898), Fuhrmann (1899), and Monticelli (1899). The name which Fuhrmann (1899:864) gave for it can be dismissed as a nomen nudum. Lühe (1898 and 1899) considered that the species belonged to *Ichthyotaenia*. It has already been shown in the discussion of the genus *Proteocephalus* that the name *Ichthyotaenia* Lönnberg (1894) is a synonym of the name *Proteocephalus* Weinland (1858) and hence cannot be retained. The latter name also antedates the name *Crepidobothrium* Monticelli (1899) and on that account should be used in place of *Crepidobothrium* if structurally Baird's species shows sufficient agreement with *Taenia flicollis* (*ambigua*) Rud. the type of *Proteocephalus*. An examination of Monticelli's (1899) description and figures and of the writer's description with its accompanying figures, shows conclusively that this species does not agree anatomically with the type of *Proteocephalus* and that this species really belongs to a different genus. The only available name is *Crepidobothrium* Monticelli (1899) which is not invalidated by the name *Crepibothrium* as used by Fuhrmann and which was unaccompanied by a diagnosis, since the word *Crepibothrium* is not a homonym of *Crepidobothrium*. Lühe's objection therefore is not valid.

One bottle of 9 specimens with heads, labelled "*Ichthyotaenia Gerrardii* (Baird) ? aus *Eunectes murinus* intestinum Berlin Aquarium" was received from Dr. Anton Collin, Berlin, in answer to a request from Professor Ward. This is now No. 10.179 in Professor Ward's collection.

One bottle of 5 specimens with heads and some pieces, labelled "*Taenia racemosa* Rud from *Eunectes murinus*." was received from A. E. Shipley, Cambridge. The material is now No. 08.472 in Professor Ward's collection. One bottle of 3 specimens with heads, labelled "*Taenia Eunectes* from Anaconda. sm. Intestine, Phila. Zoo. G. 939. U. P. Path-Hist. 1694," was received from A. J. Smith, Philadelphia. This is now No. 10.190 in Professor Ward's collection. Seven slides, one of them containing a head, labelled "No. 1858, From *Boa Constrictor* Box 53-20, 1893," were received for examination from the Bureau of Animal Industry, Washington.

A careful study of the specimens thus brought together showed that they belonged to the same species. Since in each lot one or more heads were present a careful study of this organ could be made. For this purpose balsam mounts were made from some heads while others were cleared and examined in glycerine. On account of the small amount of material the section method was not used except in a single instance. The results of this study are best shown in the accompanying table. The heads used for measurement were chosen quite at random, for an examination of the material showed that a tabulation of measurements of all heads was unnecessary. The dimensions are in millimeters.

Lot number Source Preparation		1858 B. A. I. balsam	08.472 from Shipley balsam unflattened	08.472 from Shipley glycerine	10.179 from Anton Collin glycerine	10.179 from Anton Collin glycerine	10.190 from A. J. Smith glycerine	<i>T. eunectes</i> Data from Smith (1908)
Head	breadth	1.360 <sup>a</sup>	0.935 <sup>b</sup>	1.090	1.190	1.090	1.190	1.300
	length	0.680±	0.680±	0.680±	0.680±	0.680±	0.850	0.900 <sup>c</sup>
Suckers	breadth of	0.646	0.400	0.646	0.544	0.510	0.510	0.700
	two	0.646	0.459	.....	0.544	.....	0.544	.....
Neck	breadth	1.000	0.765	0.850	0.402	0.390	1.190	0.300
	length	0.500±	0.680	0.500	0.850	0.500	0.500	1.200 <sup>c</sup>

- Head showed some effect of flattening in mounting. This may have some effect on measurements of suckers also.
- Head was evidently very strongly contracted as were also the suckers.
- Measurements were taken from Smith's drawing which was accompanied by a scale of magnification.

A study of the above table shows that in the main the measurements agree very well. Where apparent discrepancies occur they are easily accounted for by states of contraction and compression. In every case the shape of the suckers is the same, due allowances being made

for contraction and relaxation. Every head of the four lots was examined in this respect and in each sucker the lower margin was turned in thus "forming an angular intrusion into the cavity of the sucker" as Smith (1908) described it. In the more contracted or in greatly expanded suckers this condition was somewhat difficult to make out but when properly cleared as in glycerine or balsam it was apparent. A study of toto preparations of the proglottids from the various lots fails to disclose any good characters for separating them. The writer therefore bases the following description upon this material so collected together, referring at times to special lots. He also uses the descriptions by Smith (1908) and by Monticelli (1899) as sources of comparative data. It was desired to study the slides upon which Monticelli based his description but unfortunately Professor Ward was unable to secure them.

This is one of the largest of the Proteocephalid species inhabiting snakes. *O. calmettei* (Barrois), *O. marenzelleri* (Parona), *O. grandis* are of about the same size. The latter even exceeds *C. gerrardii* in some measurements. Next smaller than the members of this group comes *O. racemosa* (Rud.). A comparison of the table at the end of this report shows the size relationships of these species. The strobila varies considerably in length. According to Baird (1860) it measures 45.6 cm. (18 inches). Smith (1908) reports specimens 95-100 mm. long. Diesing (1850:511) gives its length as 2 inches to 1½ feet. Monticelli gives no data on this point. The reported breadth varies from 0.85 mm. in some short specimens examined by the writer to 1.8 mm. in the B. A. I. slide 1858, to 2.0 mm. according to Smith, and 2.0-6.0 mm. (1-3 lines) in the middle to 2 mm. (1 line) at the posterior end, according to Diesing (1850). The strobila is flat and relatively thin. The surface is more or less thrown into folds. The proglottids are attached by their full width. The segmentation is indistinct in the anterior region and more distinct in the region of mature and ripe proglottids. In certain strobilas the segmentation is more distinct than in others. It is never as clearly marked as in some species of Proteocephalids.

The head is large, readily distinguishable to the naked eye. Baird describes it in these words: "The head is large, tetragonal; the four bothria disposed crosswise, joined by the margins." Smith (1908) says of it, "The head, viewed from the front presents a crucial appearance from the prominence of the suckers, measuring transversely across the two opposed suckers 1.5 mm. and laterally across two adjacent suckers 1.3 mm. . . . The suckers, thus prominent, form the rounded arms of the crucial frontal picture, each sucker being globose in shape and having a lateral diameter of about 0.7 mm." Smith's figures of the



head are reproduced (Figs. 33, 34). Monticelli's (1899) description of the head reads: "Come si vede, il capo (Monticelli's figures of the head are reproduced in figures 123, 124) è abbastanza grande e ben distinto dal collo che anteriormente si slarga di poco come pei sostenerlo: esso ha l'aspetto grossolano di un pomo da bastone e, come si rileva dalla figura, è rigonfio e massiccio, tetragonale, a forma di piramide tronca. Anteriormente ristretto, cupuliforme, terminato nel mezzo da un indistinto cocuzzoletto apicale conoide; posteriormente slargato e troncato sporge oltre il collo per i suoi spessi margini rigonfi e presenta, nel mezzo di ciascuno dei quattro lati, una insenatura molto accentuata."

The head is always tetragonal and somewhat pyramidal. This shape may be varied to some extent by the states of contraction. A head which is relaxed and whose suckers are expanded may have a lobate appearance (Fig. 13). Here deep grooves may be seen between the suckers. In greatly contracted heads (Fig. 12) the suckers are drawn closely together, the furrows between the suckers are almost obliterated and the suckers themselves are reduced in size. In such heads the suckers are seen to be directed forward while in the relaxed head the suckers are directed outward. These figures should be compared with the drawings of heads by Smith (1908) and Monticelli (1899), which have been reproduced here (Figs. 33, 34 and Figs. 123, 124). These figures illustrate the various states of contraction which one meets in a study of considerable material. The dimensions of the head are: breadth 0.935-1.30 mm. in the writer's material, 1.75 mm. (Baird), thickness nearly equals breadth, length about 0.68-0.90 mm. The apex of the head is slightly elevated, rarely flat. There is no rostellum and no spines.

From toto preparations no trace of a fifth sucker could be found but in a series of transverse sections of the head a small sunken fifth sucker was found which had degenerated until it had lost its radial musculature (Fig. 42). The sucker still possessed its opening to the exterior which measured 0.037 by 0.026 mm. and this opening led into a cavity but a little more than 0.03 mm. deep. The sucker measured about 0.048 by 0.067 mm. on its transverse axes. From the tip it extended about 0.06 mm. into the head. This tissue was in bad condition. It took the stain poorly. Its nuclei were not visible either in the sucker or in the other parts of the head. Cell outlines were indistinct or lacking. The musculature of the sucker was irregular or perhaps no longer visible. There were however certain fibers which seemed to be muscles. A basement membrane was clearly visible and surrounding this on the outside were circular muscle fibers which could be readily distinguished by focussing on successive layers of tissue. The sucker cavity was filled

with a granular mass of unknown origin. The writer noted a similar granular material in the sucker cavities of degenerating suckers of *Ophiotaenia filaroides*. This sucker stands about midway between the vestigial sucker of *O. filaroides*, *O. lönnbergii* and *P. ambloplitis* on the one hand and the functional fifth sucker of *P. fallax*, *P. pinguis* and *P. percae* on the other. Approximately the same stage of degeneration is shown in the drawing (Fig. 44) of a degenerating fifth sucker of the plerocercus of *O. filaroides* as is shown by the fifth sucker in *C. gerrardii*.

Of the suckers Monticelli (1899) writes:

"Non vi sono botridii, ma quattro ventose, grandi ovoidali, disposte in croce, secondo il loro asse maggiore, ai quattro angoli del capo ed obliquamente e convergenti verso il cocuzzoletto apicale. Esse sono approfondate nello spessore del capo e ne occupano quasi tutta la lunghezza; fra le ventose il capo si infossa in piccoli solchi longitudinali che si terminano nelle insenature marginali innanzi ricordato. Le ventose hanno forma di ferro di cavallo, dirò meglio, ricordano la figura di un piede di cavallo ferrato visto di sotto. Esse hanno un aspetto caratteristico proprio, che può facilmente ricavarsi dalla fig. 2 e, meglio ancora, dalla fig. 3, che mostra il capo visto di sopra ed alquanto schiacciato. Chè il margine posteriore delle ventose non è integro, ma scavato da una insenatura formata dal ripiegarsi verso il mezzo del cavo di esse delle pareti posteriori della ventosa—che non formano un tutto continuo, ma sono posteriormente interrotte—che ravvicinate fra loro, costituiscono una doppia cresta, breve, la quale si perde, divaricando in due rametti a V, nel fondo della ventosa. Ma, meglio che dalla descrizione, può intendersi la peculiare struttura di queste ventose, già adombrata dal Baird, come si rileva dalle parole innanzi citate, dall' esame delle figure 2 e 3, che danno una fedele immagine della forma del capo del cestode in esame, come l'ho ricavata dallo studio del tipo originale del Baird."

Monticelli's figures above mentioned are reproduced (Figs. 123-124). In these figures the point of the inturned margin is split and each arm of the "V" is turned out. Material examined by the writer shows no such spreading of the point of the "V". A series of transverse sections show that the point of the "V" is closed. When the sucker is much relaxed the point is difficult to see, but it may be found if the head be cleared and examined in glycerine. Likewise in very strongly contracted suckers the inturned point may escape detection except when cleared and examined under favorable conditions. From an examination of three heads from Smith's material the writer is led to believe that the narrow slit-like opening in the suckers as shown in his figures (reproduced Figs. 33, 34) is due to foreshortening. Usually the opening is much more nearly round than here shown. The suckers are very prominent, most prominent in a relaxed head (Fig. 13). They measure 0.40-0.70 mm. in breadth. The average is about 0.55 mm.

A poorly defined neck region separates the head from the body. Baird (1860) says: "No distinct neck. Anterior extremity of the body very narrow." Monticelli (1899) says: "Il collo è relativamente lunghotto e le prime proglottidi sono come delle rughe e molto indistinte." A. J. Smith (1908) gives a width of 0.300 mm. for the neck and his drawing shows a length of 1.20 mm. Measurements of Smith's material however gives a width up to 1.190 mm. Measurements of six strobilas give 0.5-0.85 mm. for the length of the neck, and in these cases it is probable that the measurements given are too great. The region of proglottid formation begins very close to the head and here the proglottids are very short and their boundaries poorly defined. The neck is thin and flat. The first proglottids are much broader than long. As they become older they increase rapidly in length. Mature segments are nearly quadrate while ripe proglottids are longer than broad. The moniliform proglottids, mentioned by Smith (1908), are not characteristic of the species but are due to contraction states. Among the three specimens which he sent to Professor Ward was a short one which had these peculiarly contracted proglottids. The longest and most perfect specimens had no segments of this character nor were such proglottids observed among the specimens of the other lots. Ripe proglottids measure 1.70-2.30 mm. in length by 0.65-1.09 mm. in breadth.

The genital anlagen appear very early in the chain. In fact they are to be seen in all but the youngest proglottids. The genital aperture is irregularly alternating. It is situated near the middle of the margin of the segment. The vagina and the cirrus open into the common genital sinus, the vagina being either anterior or posterior to the cirrus-pouch. A genital sinus can scarcely be said to exist. Under favorable circumstances the sinus may be seen to be 0.020-0.030 mm. deep. This shallow sinus is easily overlooked. The opening of the vagina is sometimes dorsal to the cirrus-pouch but the writer is not prepared to say that it always occupies that position. Monticelli (1899) thinks that the vagina normally lies above the cirrus-pouch and that when it is found anterior or posterior to the same it has been displaced by pressure. From work on this species and also on several other species in which the vagina may lie in either the anterior or posterior position the writer is convinced that pressure has nothing to do with this variation. The preparations studied have all been made without compression, yet the vaginae alternate irregularly in position. Sections in a frontal plane through developing proglottids of *O. lönnbergii* show the vaginae sometimes anterior and sometimes posterior to the cirrus-pouch. They develop in those positions which they hold in mature and ripe proglottids. A careful examination of toto preparations of *C. gerrardii* and of sev-



eral species of *Ophiotaenia* shows that if the vagina is in an anterior position it extends farther anteriorly before bending toward the genital pore than it does when it occupies the posterior position. If these vaginae are displaced by pressure then they ought to show evidence of such displacement by their form or structure. This they do not do, as an examination of the drawings (Figs. 111-115) will show. It will be noted that when the vagina is anterior to the cirrus-pouch it usually crosses the coils of vas deferens. In *C. gerrardii* the vagina, when anterior, never crosses the cirrus-pouch.

The testes lie in two broad fields which tend to coalesce in the anterior region of the proglottid. Testes number about 240 in the specimens from the Bureau of Animal Industry. Monticelli (1899) found about 200 or more in each proglottid. Smith (1908) figures but 87 testes. There must be an enormous variation in the number of testes or else Smith overlooked some of them, for in a preparation of an immature proglottid from one of his specimens the writer counted nearly 400 testes. In this proglottid, delineated (Fig. 113), the testes are very small. In maturity many of them might be crowded down to a lower plane and so might be overlooked. However, in his preparations the writer has not found evidence for this crowding. There is no evidence that any of the testicular anlagen fuse together or degenerate. As a rule the testes in this species measure 0.030-0.050 mm. in diameter but in a specimen from lot 10.179 the testes measured as much as 0.080 mm. Monticelli (1899) says that they are about twice the size of the vitelline follicles. The vas deferens (Fig. 112) in ripe proglottids is thrown into numerous, heavy, spermatozoa-laden coils which extend in a mass nearly to the middle of the proglottid. Within the cirrus-pouch the ductus ejaculatorius makes a few coils before passing over into the cirrus. The latter when protruded (Fig. 114), is short, thick and very muscular. Monticelli's description agrees with this statement. The cirrus-pouch is short, broad and heavily muscled. Its length is about 0.23-0.25 mm. and its breadth about 0.10-0.15 mm. In maturing proglottids the ratio of its length to the segment breadth is 1:5 or 1:6 while in ripe proglottids it is about 1:4.

These organs (Figs. 112-115) are arranged as in the *Ophiotaenia*. The lumen of the vagina (Figs. 114, 190) near its opening to the exterior is large. The vagina is here surrounded by a strong sphincter vaginae. There are no coils of vagina anterior to the ovary. A receptaculum seminis has not been seen. Monticelli (1899) states that it is present. The ovary is bilobed and it is situated in the posterior part of the proglottid. The lobes are thick, broad and short. Their outlines are more or less irregular. An oöcapt, oötype, shell-gland, ovi-

duct, unpaired vitelline duct, lower vagina, and a uterine passage are present and these organs are arranged in the manner common to the Proteocephalidae. Monticelli (1899) gives a long and detailed description of the arrangement of these organs upon which no comments are necessary. Smith (1908) mistook these organs of the interovarial space for vitellaria.

The vitellaria are lateral loosely follicular masses which extend throughout the length of the proglottid. The follicles are small, and in some preparations they took the stain poorly. It is probable that Smith had the same difficulty in staining the vitellaria and for that reason he entirely overlooked them. Monticelli states that the vitellaria lie outside of the inner longitudinal muscle layer. The writer has examined nothing but toto preparations which perhaps are not trustworthy for the determination of this point. Nevertheless it seems that Monticelli's statement is the result of a misinterpretation of the facts. The uterus (Figs. 111, 113, 114, 115) is a median tube which in ripe proglottids (Fig. 112) has from 20 to 30 lateral outpocketings on either side. As these pouches fill with eggs they become rounded and the septa become indistinct. The uterus is not connected with the lobes of the ovary as Smith (1908) figures it. His figure is incorrect. The pouches are more numerous and more closely applied to each other and less slender than he shows them. Uterine pores were not visible in material examined by the writer. As to the method of discharging the eggs Monticelli (1899) writes: "Nelle ultime proglottidi l'utero, pregno a rimpinzato d'uova, sporge alquanto, facendo ernia contro le pareti, sulla faccia ventrale delle proglottidi. Non ho osservato orifizio esterno permante dell'utero, come quelle che Krämer ha visto in alcuni *Tetracotylus* (p. e. *T. filicollis*) [Monticelli here cites Pl. 28 fig. 42 in Krämer's paper of 1892] e neppure ho constato determinarsi uno sbocca provvisorio per dar uscita alle uova: penso, forse, l'uscita delle uova all'esterno avvenga, come in altri casi, per deiscenza."

According to Smith (1908) the six-hooked embryo measures 0.016-0.018 mm. in diameter, the two membranes 0.028-0.030 mm. and 0.085-0.100 mm. respectively. The writer was unable to measure or to study any eggs of this species hence he is not able to comment on Smith's data nor upon Monticelli's description of the eggs which is here quoted:

"Le uova uterine, relativamente piccole, hanno un guscio spesso e molto evidente: contengono già l'oncosfera involta in una veste, od invoglio, che come una teca a netto contorno e non molte spessa, per quanto ben distinta, circonda, come in altri teniadi, l'embrione. Ciascun uovo, con il relativo guscio, è racchiuso in una capsula grande, sferoidale e di diametro assai più del doppio del guscio,

omologa analoga a quella che si osserva in altri cestodi (capsule uterine, od ovariche Auct.). La quale, come altrove ho dimostrato [*Monticelli, Fr. Sav.*—Sulla cosiddetta subcuticola dei Cestodi, in: *Rend. R. Acc. Sc. Napoli*, Fasc. 7-12, Luglio-Dicembre 1892 (sul principio dove parlo dell'uovo dei Cestodi e ne riassumo lo sviluppo).] nulla ha da vedere col guscio delle uova essendo essa una formazione molto diverso, secondaria e posteriore: circa l'origine di questa, oltre quanto ho espresso nel citato mio lavoro, veggasi pure il *Diamare* [*Diamare, V.*—Il genere *Dipylidium*, in: *Atti R. Accad. Sc. Nap.* (2) Vol. VI. N. 7, 31 pp, 3 Tavole]. Capsula queste che ritengo possa e debba venir interpretata come una sorte di *cocon* e corrispondente a formazioni del genere che si osservano nelle uova di altri animali e ne circonda il guscio."

Since Smith's specimens of *Taenia eunectes* Smith came from a host which is not uncommon in American zoological gardens and since his paper will probably be widely referred to by American investigators more specific attention is called to certain misinterpretations in the description and delineation of this species by Smith (1908). His figure 4, Pl. III which has not been reproduced shows very clearly that he considered this form to be a species of *Taenia*. His attempt to make the organs of this species agree with those of *Taenia* has resulted in considerable confusion. The organ which he has labelled the vagina is the cirrus-pouch and vice-versa. The receptaculum seminis of his labelling is the mass of coils of the vas deferens. The lateral vitellaria he has omitted entirely. He labels vitellaria that mass of coils comprising the organs of the interovarial space. The ovary in this species is never connected with the uterus as he figures it, but always through the single oviduct, oötype, and uterine passage as has been figured (Figs. 99, 104). The writer has never seen the lateral pouches of the uterus in this species or in any species of *Ophiotaenia* as Smith figures them. The uterus which he figures is characteristic of *Taenia*, not of a *Proteocephalid*. Unfortunately the writer has not been able to examine a proglottid from the material received from Smith that was in the same state of development as that shown in his figure. The writer has, however, examined younger proglottids and these in every case and in every essential particular agreed with the specimens received from other sources.

There can be no doubt that Smith's specimens belong to the species *Crepidobothrium gerrardii* Monticelli, hence the name *Taenia eunectes* is a synonym of *C. gerrardii* and should be suppressed.

This is the only known species in the genus *Crepidobothrium*. It finds its nearest congeners among the larger species of *Ophiotaenia*. While in the structure of the proglottids and in the arrangement of the genital organs this species agrees almost perfectly with the *Ophiotaenia*



there remain two characters which are deemed of sufficient value to warrant a separation of the snake Proteocephalids into two genera. These characters are the structure of the suckers and the length of the neck. The first character has already been discussed. All the known species of *Ophiotaenia* have relatively long necks, i. e., 2-8 mm. long while *C. gerrardii* has a short neck. Monticelli was amply justified in separating this species from his genus *Tetracotylus*, sensu latu. However since it has been shown that his type species of *Tetracotylus* should be separated from the genus *Proteocephalus* and even from the family Proteocephalidae, his arguments in justification of his action are not repeated.

Monticelli's (1899) diagnosis of the genus *Crepidobothrium* reads:

"Capo inerme, grande, rigonfio, piramidato: ventose ellittiche, posteriormente a margine interrotto e rientrante nel cavo della ventosa. Aperture genitali marginali, irregolarmente alternanti. Orifizio dell'antro genitale subventrale, largo: sbocco della vagina dorsalmente e disotto alla tasca del pene: ovario piccolo: testicoli piccolissimi, numerosi, collocati nel mezzo della proglottide, internamente alla muscolatura longitudinale interna, in unica serie. Utero allungato, tubolare, sacciforme. Vitellogeni piccoli, numerosi, periferici. Uova avvolte in una capsula gelatinosa."

His diagnosis does not require much amplification but may be restated thus. *Crepidobothrium* Monticelli: Head large, swollen, pyramidal, tetragonal, unarmed. Fifth sucker vestigial. Suckers inversely cordate, posterior margin interrupted and re-entrant into sucker cavity. Genital aperture marginal, irregularly alternating. Vaginal opening dorsal to cirrus-pouch. Vagina anterior or posterior to cirrus-pouch. Testes in two lateral fields anterior to the ovary. Ovary bilobed, lobes irregular, relatively small. Uterus tubular, median, possessing in ripe proglottids numerous lateral outpocketings. All genital organs within inner longitudinal musculature except portion of cirrus-pouch and vagina. Eggs small, provided with three(?) membranes, outer one gelatinous.

*Type of genus*:—*Crepidobothrium gerrardii* (Baird) from *Boa constrictor* L. (type host); So. America (Brazil) (type locality).

In the following table (pages 260-267) the principal data relating to the species of *Ophiotaenia* and *Crepidobothrium* are brought together:

Comparative Table of Selected Characters of Species of *Ophiotaenia* and *Crepidobothrium*

Characters	<i>Ophiotaenia filaroides</i> La Rue	<i>O. lönnbergii</i> (Fuhrmann)	<i>O. nattereri</i> (Parona)	<i>O. perspicua</i> La Rue
Strobila	8.0-11.0 cm. long x 0.8-0.9 mm. broad at widest part	17-19 cm. long x 1.35 mm. broad at widest part	7.5-25 cm. long x 1 mm. broad at widest part	36 cm. long x 2.0 mm. broad at widest part
Neck	3-4 mm. long, narrow	2 mm. long x 0.375-0.54 mm. broad	Long, 7-8 times the length of head, breadth not known	5-7 mm. long x 0.17-0.425 mm. broad
First proglottids	0.1-0.17 mm. long x 0.3-0.36 mm. broad	0.05 mm. long x 0.5 mm. broad	Broader than long	Much broader than long.
Mature proglottids	Quadrate or longer than broad	0.85-1.0 mm. square or more elongated. May be as much as 2.5 mm. long x 0.45-0.5 mm. broad	Length about equal to breadth	2 mm. square or longer than broad
Ripe proglottids	1.6 mm. long x 0.8 mm. broad to 4.0 mm. long x 0.75 mm. broad	.....	2.0 mm. long x 0.33-0.50 mm. broad	Largest proglottid measured 3.8 mm. long x 1.2 mm. broad
Head	Globose, flattened dorsoventrally, apex conical 0.366-0.46 mm. broad	Globose, flattened dorsoventrally. 0.5-0.6 mm. broad	Rounded but not spheroidal. 0.24-0.25 mm. broad	Conical, flattened dorsoventrally, cut by deep grooves. 0.355-0.408 mm. broad
Suckers (the four)	Oval, with deep cavities. Max. dimension 0.165-0.184 mm.	Prominent, oval, cavities deep. Dimensions 0.24-0.26 mm. long x 0.14-0.22 mm. broad	Circular, cavities deep, margins heavy. Diameter 0.12-0.15 mm.	Circular, oval or somewhat triangular. 0.105-0.17 mm. in maximum dimension
Fifth Sucker	Vestigial, deep set in tissues of head	Vestigial, deep set in tissues of head	Not present? If present must be vestigial	Vestigial, deep set in tissues of head
Genital pore, location on margin of segment	At end of first fifth of proglottid	At end of first third to two-fifths of proglottid	A little anterior to middle of proglottid	At end of first third to half
Cirrus-pouch, size	0.22 mm. long x 0.11 mm. broad	0.185-0.28 mm. long x 0.05-0.085-0.1 mm. broad	0.265-0.28 mm. long	0.255-0.32 mm. long x 0.08-0.09 mm. broad
Cirrus-pouch, length into breadth of segment	3-4 times	3-5 times	3-3½ times	3-4 times

Comparative Table of Selected Characters of Species of *Ophiotaenia* and *Crepidobothrium* (Continued)

Characters	<i>Ophiotaenia filaroides</i> La Rue	<i>O. lönnbergii</i> (Fuhrmann)	<i>O. nattereri</i> (Parona)	<i>O. perspicua</i> La Rue
Ductus ejaculatorius	With few coils	In several coils	In many coils	In several coils
Testes, number	70-114	90-160	80-100	150-215
Testes, size	0.05-0.06 mm. in diameter	0.05-0.08-0.12 mm. in diameter	0.042 mm. in diameter	0.053-0.106 mm. in diameter
Testes, arrangement	In 2 lateral fields	In 2 lateral fields, reaching laterad of excretory vessels	In 2 lateral fields	In 2 lateral fields
Vagina, relation of, to cirrus pouch	Anterior to cirrus-pouch, never crossing latter	Anterior or posterior, never crossing cirrus-pouch	Anterior or posterior to cirrus-pouch, frequently crossing or lying dorsal to latter	Anterior or posterior to cirrus-pouch, never crossing latter
Uterus, pouches on either side	20-35	25-40	15-20	20-30
Embryo, size	Diameter 0.21 mm.	Yolk-mass 0.01-0.012 mm. in diameter	Egg 0.024 mm. in diameter	0.018-0.021 mm. in diameter
Eggs, number and size of membranes	Three membranes, outer one 0.035-0.1 mm., second and 0.03 mm. in diameter	.....	.....	Three membranes, outer one 0.045-0.1 mm. in diameter
Additional data	8-12 uterine pores. Excretory ducts straight	Main excretory ducts pass through the segments as spirals	Protruded cirrus heavy at base, slender at tip, 0.2-0.21 mm. long	Protruded cirrus slender, 0.2 mm. long
Hosts	<i>Amblystoma tigrinum</i>	<i>Necturus maculosus</i>	<i>Coluber</i> sp.	<i>Natrix rhombifer</i>
Locality	Nebraska, Kansas	Ohio, Indiana	Liguria, Italy	Illinois, Oklahoma
Chief sources of data	LaRue (1909)	Fuhrmann (1895), the present paper	Parona (1901), Schwarz (1908), the present paper	The present paper



Comparative Table of Selected Characters of Species of *Ophiotaenia* and  
*Crepidobothrium* (Continued)

Characters	<i>O. lactea</i> (Leidy)	<i>O. racemosa</i> (Rudolphi)	<i>O. pigmentata</i> (von Linstow)
Strobila	38.6 cm. long x 1.4 mm. broad when alive, 19.3 cm. long x 2.1 mm. broad when preserved	16 cm. long x 1 mm. broad	32 mm. long x 1.78 mm. broad
Neck	Moderately long	.....	Very long
First proglottids	Broader than long	.....	0.13 mm. long x 1.1 mm. broad
Mature proglottids	Longer than broad	.....	.....
Ripe proglottids	.....	2 mm. long x 1 mm. broad	.....
Head	Small	0.54 mm. broad	Rounded, about 0.5 mm. broad x 0.57 mm. long
Suckers (the four)	Hemispherical	Circular, 0.27-0.3 mm. in diameter	Circular. 0.18 mm. in diameter
Fifth Sucker	.....	No functional fifth sucker present	Apparently not present
Genital pore, location on margin of segment	Marginal	At end of first third	.....
Cirrus-pouch, size	.....	.....	.....
Cirrus-pouch, length into breadth of seg-	.....	About 2 times	.....

Comparative Table of Selected Characters of Species of *Ophiotaenia* and  
*Crepidobothrium* (Continued)

Characters	<i>O. lactea</i> (Leidy)	<i>O. racemosa</i> (Rudolphi)	<i>O. pigmentata</i> (von Linstow)
Ductus ejaculatorius	.....	Sinuuous	.....
Testes, number	.....	100-120	.....
Testes, size	.....	0.072-0.078 mm. in diameter	.....
Testes, arrangement	.....	In 2 lateral fields, not completely separated	.....
Vagina, relation of, to cirrus-pouch	.....	Anterior or posterior to cirrus-pouch	.....
Uterus, pouches on either side	.....	20	.....
Embryo, size	.....	Egg 0.024 mm. in diameter	.....
Eggs, number and size of membranes	.....	Three membranes	.....
Additional data	.....	Testicular field not interrupted at either end of segment	Tissue filled with darkly pigmented chalk-bodies
Hosts	<i>Natrix sipedon</i>	<i>Coluber</i> sp., <i>Ophiomorphus miliaris</i> , <i>Ophis merremii</i>	<i>Psammodynastes pulverulentus</i>
Locality	Locality not stated; probably eastern United States	Brazil	Java (Semarang)
Chief sources of data	Leidy (1855)	Schwarz (1908)	von Linstow (1908)

Comparative Table of Selected Characters of Species of *Ophiotaenia* and  
*Crepidobothrium* (Continued)

Characters	<i>Ophiotaenia trimeresuri</i> (Parona)	<i>O. calmettei</i> (Barrois)	<i>O. punica</i> (Cholodkovski)
Strobila	10.5 cm. long x 0.75-1.5 mm. broad at widest part	27-40-80 cm. long x 0.97-1.2-2.0 mm. broad	10.0 cm. long x 2-2.75 mm. broad
Neck	3 times length of head, 0.25-0.5 mm. broad	4-5-8 mm. long x 0.58-0.98 mm. broad	Very short
First proglottids	Broader than long	Much broader than long	Broader than long
Mature proglottids	About square or longer than broad	About 0.85 mm. square	Quadrate or longer than broad
Ripe proglottids	No fully ripe proglottids seen. (La Rue)	2-3-4 mm. long x 1-1.2 mm. broad	.....
Head	0.75 mm. broad	Somewhat spheroidal or tetragonal, 1.0-1.3 mm. broad, 0.6 mm. long, 0.935 mm. thick	Somewhat tetragonal, 1.5 mm. broad
Suckers (the four)	Prominent, hemispherical, muscular, 0.16-0.25 mm. in diameter	Globular, 0.27-0.3-0.408 mm. in diameter. Cavity deep, 0.12-0.17-0.185 mm. in diameter	Round, muscular, 0.7 mm. in diameter. Inner wall thicker than outer
Fifth Sucker	Not present. Vestigial?	Not present. Vestigial?	Not present. Vestigial?
Genital pore, location on margin of segment	At end of first third	At or near middle	Near middle
Cirrus-pouch, size	0.27-0.33 mm. long x 0.136 mm. broad	0.25-0.29-0.33 mm. long x 0.1-0.136 mm. broad	.....
Cirrus-pouch, length into breadth of segment	2½-4 times	5-6 times in mature and 4 times in ripe segments	3-4 times



Comparative Table of Selected Characters of Species of *Ophiotaenia* and *Crepidobothrium* (Continued)

Characters	<i>Ophiotaenia trimeresuri</i> (Parona)	<i>O. calmettei</i> (Barrois)	<i>O. punica</i> (Cholodkovski)
Ductus ejaculatorius	In many coils	With numerous coils	.....
Testes, number	100-108	130-160	200
Testes, size	0.063-0.08 x 0.027 mm.	0.026-0.04-0.06 x 0.053 mm.	.....
Testes, arrangement	In 2 lateral fields, not near vitellaria	In 2 lateral fields	In 2 well defined lateral fields
Vagina, relation of, to cirrus-pouch	Anterior or posterior to cirrus-pouch, not crossing latter	Anterior or posterior, sometimes opening dorsal to cirrus-pouch, not crossing latter	.....
Uterus, pouches on either side	20-30?	24-35	Not seen
Embryo, size	.....	0.212 mm.	.....
Eggs, number and size of membranes	.....	Three membranes, second one 0.022-0.024 mm., inner 0.014 mm. in diameter	.....
Additional data	Many coils of ductus ejaculatorius in base of protruded cirrus	Genital sinus shallow, Vagina broad near genital sinus	Vitellaria appearing granular in toto preparations
Hosts	<i>Trimeresurus formosus</i>	<i>Lachesis (Bothrops) lanceolatus</i>	Dog (?). Probably a snake
Locality	Island of Mentawai, East Indies	Martinique; São Paulo, Brazil	Island of Dscherba, Tunis
Chief sources of data	Parona (1898), Schwarz (1908), the present paper	Barrois (1898), Marotel (1898), Schwarz (1908), the present paper	Cholodkovski (1908)

Comparative Table of Selected Characters of Species of *Ophiotaenia* and *Crepidobothrium* (Continued)

Characters	<i>O. marenzelleri</i> (Barrois)	<i>O. grandis</i> La Rue	<i>Crepidobothrium gerardi</i> (Baird)
Strobila	40 cm. long x 1.2-2.0 mm. broad	Fragments measured 2.75-4.25 mm. broad at widest part and 20 cm. long	9.5-45.6 cm. long x 0.85-2.0-6.0 mm. broad
Neck	.....	4-8 mm. long x 0.85-1.0 mm. broad	Very short and broad. 0.5-0.8 mm. long x 0.3-1.19 mm. broad
First proglottids	.....	Much broader than long	Much broader than long
Mature proglottids	.....	Usually longer than broad	Nearly square
Ripe proglottids	Largest ripe segments 5.5 mm. long x 1.5-2.0 mm. broad	Usually longer than broad. 3.5 mm. long x 2.3 mm. broad. Longest segment measured 8 x 2.75 mm.	1.7-2.3 mm. long x 0.65-1.9 mm. broad
Head	Round, muscular, 1.5-2 mm. broad	Somewhat conical, base swollen and merged with neck, 1-1.2 mm. broad, 0.5-0.6 mm. long	Somewhat tetragonal and pyramidal, 0.93-1.3-1.75 mm. broad, flattened dorsoventrally, 0.68-0.9 mm. long
Suckers (the four)	Round, prominent, 0.6-0.7 mm. in diameter	Circular, not prominent, 0.34-0.35 mm. broad x 0.35-0.36 mm. long	Prominent, muscular, coracate with lower margin interrupted and re-entrant into cavity. 0.4-0.7 mm. broad
Fifth Sucker	Not present. Vestigial?	Not present. Vestigial?	Small, degenerate and sunken, still possessing an opening to exterior
Genital pore, location on margin of segment	Near middle	Near middle	Near middle
Cirrus-pouch, size	Large	0.64-0.75 mm. long x 0.24-0.26 mm. broad	0.23-0.5 mm. long x 0.1-0.15 mm. broad
Cirrus-pouch, length into breadth of segment	3 times	3-5 times	4-5.6 times

Comparative Table of Selected Characters of Species of *Ophiotaenia* and *Crepidobothrium* (Continued)

Characters	<i>O. marenzelleri</i> (Barrois)	<i>O. grandis</i> La Rue	<i>Crepidobothrium gerardi</i> (Baird)
Ductus ejaculatorius	Somewhat coiled	Nearly straight	With several coils
Testes, number	150-200-240	200-250	200-400
Testes, size	0.06-0.07 mm. in diameter	0.04-0.05 x 0.075-0.1-0.125 mm.	0.035-0.05-0.08 mm. in diameter
Testes, arrangement	In 2 lateral fields	In 2 broad lateral fields	In 2 lateral fields
Vagina, relation of, to cirrus-pouch	Usually posterior to cirrus-pouch	Anterior or posterior to cirrus-pouch	Anterior or posterior to cirrus-pouch; vagina opens dorsal to latter
Uterus, pouches on either side	20-25	40-60	20-30
Embryo, size	.....	0.015-0.016 mm. in diameter	0.016-0.018 mm. in diameter
Eggs, number and size of membranes	Two membranes	Three membranes, outer one 0.026 x 0.037 or 0.032 mm. in diameter, second 0.021-0.023 mm.	Three membranes, outer one 0.085-0.1 mm., second 0.028-0.03 mm. in diameter
Additional data	Protruded cirrus long and slender, swollen at base, filiform at tip, 1 mm. long. Some coils of ductus in swollen base	Protruded cirrus short and heavy, containing no coils of ductus ejaculatorius in base	Fifth sucker visible only in sections
Hosts	<i>Ancistrodon piscivorus</i>	<i>Ancistrodon piscivorus</i>	<i>Eunectes murinus</i> , <i>Boa constrictor</i>
Locality	Southern United States	Southern United States	Brazil
Chief sources of data	Barrois (1898), Schwarz (1908)	The present paper	Baird (1861), Diesing (1850, also 1864), Monticelli (1899), Smith (1908), the present paper



## OÖCHORISTICA CRYPTOBOOTHRIUM (von Linstow) La Rue

1906:	<i>Ichthyotaenia cryptobothrium</i>	von Linstow	1906:185
1911:	<i>Oöchoristica cryptobothria</i>	La Rue	1911:481

Under the name of *Ichthyotaenia cryptobothrium* von Linstow (1906) described a cestode from the intestine of a tree-snake, *Chrysopelea ornata* Russell, Kurunegala. La Rue (1911) stated, but without assigning reasons therefor, that this species did not belong in the genus *Ichthyotaenia* or *Proteocephalus* but in the genus *Oöchoristica* Lühe.

A careful examination of von Linstow's description and figures shows that this species cannot belong to the *Proteocephalidae*. The position of the vitellaria in the *Proteocephalidae* as, indeed, in the whole order of the *Tetraphyllidea* is lateral, the vitellaria extending nearly the full length of the proglottid. In this species the vitellaria are globular masses lying just posterior to the ovary. This relation occurs in the *Cyclophyllidea*. Species of *Oöchoristica* Lühe show this relation and since this genus includes other species of cestodes parasitic in snakes it seems probable that von Linstow's species belongs here. La Rue (1911) therefore proposed for it the specific name *Oöchoristica cryptobothria* (von Linstow) La Rue. The specific name should end in "ium" not "ia" as he made it.

Unless the invaginated or infolded condition of the head is a constant feature it can have neither generic nor specific importance. Apparently not enough is known concerning the heads of this species to establish the value of this condition as a diagnostic character.

## MONTICELLIA CORYPHICEPHALA (Monticelli) La Rue

[Figs. 94-96, 132, 181, 186]

1891:	<i>Tetracotylus coryphicephala</i>	Monticelli	1891:151-174
1894:	<i>Ichthyotaenia coryphicephala</i>	Lönnberg	1894:803
1896:	<i>Ichthyotaenia coryphicephala</i>	Riggenbach	1896:267
1900:	<i>Ichthyotaenia coryphicephala</i>	Braun	1894-1900:1680-1681
1911:	<i>Monticellia coryphicephala</i>	La Rue	1911:474

Specific Diagnosis: Characters of genus. Head dilated, somewhat triangular or globose, when seen from the front swollen, sub-quadrate,

anteriorly elongated to form a conical elevation, unarmed and not very prominent, distinct from neck. Breadth of head perhaps 0.35 mm. Suckers four, fairly prominent, oval in shape, about 0.15 mm. long, situated at four angles of head. No fifth sucker. Neck very long, narrow. First proglottids short, middle ones almost rectangular, posterior and last ones decidedly rectangular, swollen in the middle. Ripe proglottids about 1.80-2.0 mm. broad by 0.68-1.0 mm. long by about 0.34 mm. thick. Proglottids attached by full width. Intersegmental furrows shallow. Corners of proglottids not marked. Segmentation indistinct.

Genital organs as in genus. Genital pore marginal, irregularly alternating in first one-fourth or one-fifth of proglottid length. No genital papilla. Testes spheroidal, 0.05-0.085 mm. in maximum dimension, numerous, 100 or more, situated in single dorsal field outside of inner longitudinal muscle sheath. Vas deferens a mass of coils inside the inner muscle sheath. Cirrus-pouch 0.286-0.315 mm. long by 0.094-0.105 mm. broad. Length of cirrus-pouch 5 to 6 to  $6\frac{1}{2}$  times into proglottid breadth. Ductus ejaculatorius describing numerous coils. Cirrus slender, unarmed. Vagina and vaginal opening always anterior to cirrus-pouch. Vagina never crossing latter. Sphincter vaginae and receptaculum seminis present. Vagina within inner muscle sheath. Vitellaria lateral, extensive, ventral, follicles forming a single layer in cortical parenchyma. Ovary posterior, bilobed, augmented by large protuberances, projecting dorsally, partially outside of inner muscle sheath. Organs of interovarian space as in Proteocephalidae. Uterus with many long slender lateral outpocketings, ventral, and outside of inner muscle-sheath. Egg-membranes not observed. Embryos 0.015-0.017 mm. in diameter.

Habitat: Intestine of *Silurus* sp., locality not stated.

Type: Slides in collection of Monticelli, from specimen No. 571 in the Zoological Museum at Vienna.

This species was first described from *Silurus* sp. by Monticelli (1891:151-174). For this and nineteen other species of cestodes from fish he proposed the genus *Tetracotylus*, without, however, naming a type species. That genus was based on *Taenia coryphicephala*, the species which he described most completely. Lönnberg (1894:803) listed this as one of the species of *Ichthyotaenia* without entering into a discussion of its anatomy. Riegenbach (1896:267) listed this among the species of *Ichthyotaenia*. Braun (1894-1900:1680-1681) states that Monticelli's genus *Tetracotylus* is based on the species *Taenia coryphicephala* but that the generic name suggested by Monticelli is a homonym of the name *Tetracotyle* suggested by Filippi (1854). He said moreover that

*Tetracotylus* had been used in place of *Tetracotyle*. For these reasons the name *Ichthyotaenia* should be used in place of it.

La Rue (1911:474) established for this and certain other species the genus *Monticellia* and the family *Monticellidae*.

This study is based upon data secured from Monticelli's (1891) paper and also upon Monticelli's type slides which Professor H. B. Ward very kindly secured for study. This material originally came from the zoological museum at Vienna. The host of the species is *Silurus* sp.

Monticelli (1891) is quoted on the external characters for the writer has examined only prepared slides of this species:

"Capo slargato subtriangolare, visto di fronte, rigonfiato, subquadrato, anteriormente allungato a formare un cocuzzolo conico, inerme, non molto proeminente, ben distinto dal collo. Le quattro ventose mediocri non molto proeminenti, disposte ai quattro angoli del capo. Collo lunghissimo, ristretto. Prime proglottidi brevi, mediane subrettangolari, posteriori ed ultime decisamente rettangolari, rigonfie nel mezzo. Aperture genitali marginali irregolarmente alternanti."

Monticelli (1891) gives no dimensions of the head, neck and strobila.

One of Monticelli's slides showed the head of *Tetracotylus coryphcephala* in toto. This head which had been badly compressed and somewhat broken by that treatment measured 0.459 mm. broad. This dimension, however, is too great and it seems that the normal head would not measure over 0.35 or perhaps 0.375 mm. The head should be described as somewhat globose rather than sub-triangular. The suckers could not be measured except in length which was about 0.150 mm. Monticelli's drawing of the head (Fig. 132) shows that the suckers are irregularly oval in shape, the longitudinal axis of the suckers being the greater. The neck in this slide was too badly crushed to permit accurate measurement. It was cut off 3 or 4 mm. from the head and showed no traces of segmentation. No young proglottids were to be found in the slides examined by the writer. Four representative ripe proglottids were measured. Their dimensions were 1.95 mm. broad by 0.68 mm. long, 1.85 by 0.75 mm., 2.0 by 0.75 mm., 1.80 by 1.0 mm. Transections of ripe proglottids are about 0.34 mm. thick. The proglottids are attached by their full width. The angles of the segments can scarcely be seen and the intersegmental furrows are very shallow. These observations were made on a limited amount of material so it is possible that some of the statements just made would require modification if considerable good material could be examined.

The genital pore (Figs. 95, 186) is marginal, irregularly alternating and situated at the end of the first one-fifth to one-fourth of the



proglottid. There is no genital papilla. The genital pore (Fig. 181) leads into a small genital atrium into which both cirrus-pouch and vagina open. The vagina always lies anterior to the cirrus-pouch and its opening is also clearly anterior to the opening of the male ducts. Monticelli notes a sort of sphincter muscle about the genital atrium (Fig. 181). He states that this sphincter draws the opening of the vagina and cirrus-pouch very closely together.

The testes are spheroidal. They measure from 0.05 by 0.05 to 0.05 by 0.06 to 0.07 by 0.085 mm., number about 100 or even more, and are situated (Fig. 95) dorsally in a field which covers the entire proglottid except that region occupied by the ovary and by a narrow strip on either lateral margin of the segment. There is no free median zone as Monticelli states and as he shows in his figure, reproduced (Fig. 186). His statement that they are not numerous is incorrect. The testes (Fig. 94) are outside of the inner longitudinal muscle layer, a condition which does not occur in any species of the Proteocephalidae nor, so far as can be ascertained by the writer, in any family of Tetraphyllidae. A careful study of Braun's (1894-1900) great monograph on the cestodes gives no reason for believing that this condition has been observed heretofore in any *order* of cestodes. In the Pseudophyllidae he states definitely that the testes occur in the medullary layer. He makes the same statement for the Tetraphyllidae and the Cyclophyllidae. And as for the genital organs in the Diphyllidae and the Trypanorhyncha he states that they are as in the Tetraphyllidae. The location of the testes in this species then is unique.

The vasa efferentia have not been observed. The vas deferens forms an elongated mass of coils which extends from the cirrus-pouch toward, but not reaching, the mid-field. This mass of coils lies just a little posterior to the cirrus-pouch and within the layer of inner longitudinal muscles. The duct of the vas deferens is not of uniform diameter throughout but is narrow in its beginning region then dilated and again constricted just before entering the cirrus-pouch. With its swollen coils the vas deferens functions as a vesicula seminalis. The cirrus-pouch (Fig. 181) is somewhat muscular, its muscles best developed near the outer end. Its length varies from 0.286 to 0.315 and even to 0.340 mm. and its breadth from 0.094 mm. in the longer pouches to 0.105 mm. in the shorter ones. The pouch tapers frequently to a blunt point at the inner end and is usually broadest near its opening. Its length goes 5 to 6 or  $6\frac{1}{2}$  times into the proglottid breadth. The ductus ejaculatorius (Fig. 181) is slender and has thin walls. It makes numerous intricate coils before passing over into the cirrus. The protruded cirrus has not

been observed. As the cirrus appears in the cirrus-pouch it is weakly muscular, not large, and is not armed. Probably when evaginated it would be long, slender, and without a thick base.

As seen in a toto preparation the female organs appear to be arranged in general as in the Proteocephalidae but a careful comparison of this species with any Proteocephalid reveals striking differences. The vagina (Fig. 95) always lies anterior to the cirrus-pouch and it never crosses the latter nor does it cross the mass of coils of vas deferens except in rare cases and then it crosses on the ventral side of only the most anterior coils. Monticelli states that it crosses the coils of vas deferens dorsally. The opening of the vagina is always clearly anterior to the opening of the cirrus-pouch. In a number of species of Proteocephalus and also of Ophiotaenia the opening is dorsal to the cirrus-pouch, and the writer is inclined to believe that if the remaining species of these genera were carefully investigated with that point in view many of these too would show the opening of the vagina dorsal to the cirrus-pouch. Near the vaginal opening is a weak sphincter vaginae. Beyond the sphincter the lumen of the vagina dilates slightly for a distance, perhaps 0.3 mm., then it is constricted. After arriving in the mid-field of the proglottid the vagina again dilates considerably. This dilatation persists through several curves and coils until the vagina is just about to enter the interovarial space when the vagina is greatly constricted. The dilated region is the receptaculum seminis which is much more marked than in any species of Proteocephalus observed by the writer. As shown in transections (Fig. 94) the vagina, except its beginning portion, lies within the internal layer of longitudinal muscles. In this respect *Monticellia coryphicephala* agrees with the Proteocephalidae.

The ovary (Fig. 95) is posterior and bilobed. A narrow, thin mid-piece connects the lobes which are long and broad. From the dorsal surface of the distal region of each lobe rounded prominences arise and extend toward the dorsal surface of the proglottid. Many of these prominences when observed in toto preparations seem to have no connection with the ovary and are readily mistaken for testes but when studied in transections they are seen to be a part of it. Monticelli's drawing which is reproduced (Fig. 186) does not truly represent this appearance. These dorsal prominences and the greater part of the ovarian lobes (Fig. 96) from which they arise lie in the cortical parenchyma outside of the internal layer of longitudinal muscles. The mid-piece and part of the lobes of the ovary lie within the muscular sheath. Monticelli (1891) failed to point out this condition. Here is a relation

the like of which the writer has been unable to find elsewhere in all the cestodes. So far as he is able to determine the ovary of other cestodes always lies in the medullary parenchyma.

At the posterior margin of the ovarian mid-piece is situated the oöcapt. This organ was called the "sfintere ovarico" by Monticelli. The oöcapt leads into the oviduct which after making several coils receives the vagina. Then as a fertilization passage the oviduct continues until it reaches the oötype which is surrounded by the shell glands. Just before entering the oötype the oviduct receives the unpaired vitelline duct. The oötype discharges into the uterine passage which passes ventral to the ovary and then discharges into the uterus. It will be seen from a comparison of the above description with drawings and descriptions of similar organs in the Proteocephalidae that there is marked agreement between Monticellia and the Proteocephalidae in these relations. However this is no more than can be reasonably expected when it is remembered that practically the same plan for these organs is followed throughout the whole order of Tetraphyllidea to which Monticellia and Proteocephalus belong. Monticelli (1891) takes occasion to point out what seems to be misinterpretations on the part of von Linstow (1891) in describing these organs in *Taenia longicollis*. The writer agrees with Monticelli in considering that von Linstow has mistaken the oöcapt for the oötype. A farther discussion of this point will be found in the description of *Proteocephalus longicollis*.

The vitellaria, which in the Proteocephalidae are lateral, follicular masses, the individual follicles of which are closely grouped about a central conducting tubule, are in *Monticellia coryphicephala* (Fig. 95) widely scattered lateral follicular masses which lie in a single ventral layer. In Proteocephalids the vitellaria are within the inner longitudinal muscle layer while in *M. coryphicephala* they lie outside of those muscles. The vitellaria are not only ventral but at the margin of the proglottid they turn up toward the dorsal surface, hence when viewed in a toto preparation the vitellaria at the margins seem greatly compacted. Transections (Fig. 94) of the proglottids show the method of arrangement of the vitellaria. The lateral longitudinal vitelline ducts have not been seen on account of the poor histological condition of the material. The paired vitelline ducts however, may be seen to arise in the lateral fields and to pass toward the middle of the proglottid outside of the longitudinal muscle layer. After running for some distance in this relation the ducts turn dorsally and enter within the muscle layer and then they pass on to the middle of the proglottid where the paired vitelline ducts unite to form the unpaired vitelline duct which discharges into the oötype. In all the known species of Proteocephalidae the vitel-



line ducts are always within the longitudinal muscle layer. Monticelli failed to note the position of the vitelline ducts in *M. coryphicephala*.

The uterus (Fig. 95) in ripe proglottids is made up of about 18-30 slender out-pocketings, which extend well toward the margins of the proglottids but not as far laterad as in certain species of *Proteocephalus* such as *P. fallax*, *P. dubius*, and *P. ambloplitis*. Monticelli (1891) states that the uterus when filled with eggs causes the ventral surface of the proglottid to belly out. Unfortunately his drawing showing that condition has not been reproduced. The uterus (Fig. 94) is ventral and it too lies outside of the internal layer of longitudinal muscles. Uterine pores have not been observed. Monticelli says that they do not exist but that when the uterus is full the ventral body wall ruptures, thus discharging the eggs. A careful study of good material would probably show the presence of one or more uterine pores such as was found by Krämer (1892), Schneider (1905) and by the writer in a large number of *Proteocephalids*. Monticelli gives no measurements of the uterine eggs. He states that the membranes are quite delicate and that the uterine eggs are very small. In one of Monticelli's slides a broken proglottid rendered some of the eggs visible. The spheroidal embryos measured about 0.015 to 0.017 mm. in diameter. The membranes had become so transparent that they could not be measured.

In the above description and in the drawings mentioned it has been shown that *Monticellia coryphicephala* differs from the *Proteocephalidae* and especially from the typical species of *Proteocephalus* in a number of characters which concern the position of the genital organs and their relation to the inner longitudinal muscle layer. In all the *Proteocephalids* which have been sufficiently investigated to determine these points the entire genital apparatus with the exception of a portion of the cirrus-pouch and vagina lies within the inner longitudinal muscle layer. Moreover, the follicles of the vitellaria are closely packed about a central duct. In *Monticellia* the vitellaria are in two broad lateral fields the follicles of which are scattered in a broad single layer. The paired vitelline ducts for a considerable distance lie outside the inner muscle layer. The testes and uterus are entirely outside this muscle layer and the ovary is partly outside of it. As in the *Proteocephalidae* the vagina, vas deferens and part of the cirrus-pouch are within the inner muscle layer. On account of these marked differences between the *Proteocephalidae* and the form which Monticelli named *Tetracotylus coryphicephala* the writer (1911:474) has seen fit to establish a new genus *Monticellia* in honor of Professor Monticelli.

The status of Monticelli's generic name *Tetracotylus* has already been reviewed in the introductory section where the new genus has been

defined as has also the new family Monticellidae. In this genus and family probably belong *Tetracotylus diesingii* Monticelli, *T. macrocotylea* Monticelli and *Taenia malopteruri* Fritsch. These three species are all parasitic in the Siluridae. Perhaps *Taenia osculata* Goeze belongs here also. It seems preferable, however, for the present to consider this last as a species inquirenda in the genus *Proteocephalus* in which it has long been considered to belong. More careful study into the morphology of *Taenia osculata* is desirable in order that its systematic position may be determined.

#### MONTICELLIA MACROCOTYLEA (Monticelli)

[Fig. 125]

1891:	<i>Tetracotylus macrocotylea</i>	Monticelli	1891
1896:	<i>Ichthyotaenia macrocotylea</i>	Riggenbach	1896:267
1911:	<i>Monticellia macrocotylea</i>	La Rue	1911:474

This species was described by Monticelli (1891). Lack of sufficient good material prevented a careful study of it. Riggenbach (1896:267) listed this form in the genus *Ichthyotaenia*. La Rue (1911:474) included this species in the genus *Monticellia*. Monticelli's original description is here quoted: "TAENIA MACROCOTYLEA.—Questa *Taenia*, che indico così dalle sue proeminenti ventose, ha molte rassomiglianze con le due seguenti, ma da entrambe si distingue per la caratteristica forma del capo che è nettamente distinto dal collo e per il collo più breve. Le aperture genitali sono marginali irregolarmente alternanti. Lo stato dell'individuo che posseggo non mi ha permesso uno studio più minuzioso di questa *Taenia*. \* \* \* \* \*

*Habitat*: intestino del *Silurus megacephalus*."

Professor H. B. Ward very kindly secured Monticelli's type slides of this species for examination. As a result of this examination the writer is able to add the following data to the original description.

The head of this specimen is slightly crushed. In this condition it measures 1.10 mm. broad, a figure which is probably too large by 0.10-0.20 mm. Its length is about 0.90 mm. The suckers are prominent and heavily muscled. They measure 0.45 to 0.50 mm. in diameter. The sucker cavity could not be measured. The neck is about 0.50 mm. broad just back of the head. Its length could not be ascertained for it was broken off. Mature proglottids measure about 0.75 mm. square. No young or ripe proglottids could be seen. The segmentation is distinct.

The genital pore is marginal, irregularly alternating, and situated in the first one-fourth of the proglottid. It is rendered prominent by a

small genital papilla. The length of the cirrus-pouch and the relations of the latter with the vagina could not be ascertained. The testes number about 100 or more, and they are situated in a single field between the vitellaria. The vitellaria are lateral follicular organs, the follicles of which are scattered much as they are in *Monticellia coryphicephala*. The ovary is bilobed, and it occupies a posterior position on the proglottid. The material, however, is too poor to permit of a careful study of this organ. The uterus could not be seen.

This species belongs in the genus *Monticellia* La Rue. It is differentiated from the other species of the genus by reason of its larger head and suckers, its prominent genital pore and its evident segmentation. Unfortunately the material is so poor that a careful study is not permitted and as a consequence its exact relation to the other species of the genus cannot be determined.

#### MONTICELLIA DIESINGII (Monticelli)

[Fig. 157]

1891: <i>Tetracotylus diesingii</i>	Monticelli	1891
1896: <i>Ichthyotaenia diesingii</i>	Riggenbach	1896:267
1911: <i>Monticellia diesingii</i>	La Rue	1911:474

This species was very inadequately described by Monticelli (1891) whose material was too limited and too poor to permit a careful study. Riggenbach (1896:267) listed it as one of the species of *Ichthyotaenia* but gave no description of it. La Rue (1911:474) included this form among the species of *Monticellia*. Monticelli's original description is here quoted: "TAENIA DIESINGII.—Capo subgloboso anteriormente rotundato appena distinto dal collo. Le quattro ventose grandi, proeminente e molto muscolari. Collo assai lungo: prime proglottidi brevissime appiattite, proglottidi mediane alquanto rigonfie all'aspetto cerciniformi, posteriori rettangolari, ultime subquadrate. Aperture genitali irregolarmente alternanti. L'apparato genitale, da quanto mi è riuscito vedere, si assomiglia a quello della *T. coryphicephala*.

*Habitat*: intestino del *Silurus dargado*."

Thanks to Professor H. B. Ward the writer has been able to examine Monticelli's type slides of this species and can add the following data to the original description.

The head is about 0.30 mm. in breadth. Suckers measure about 0.17 mm. in their maximum dimension while the opening of the same is about 0.08 mm. long. The musculature of the sucker is thick. Altho



the neck of this specimen is broken into several pieces, its pieces total about 3-5 mm. in length. The young proglottids are about 0.05 mm. long by 0.34 mm. broad. Fully mature proglottids are about 0.80 mm. broad by 0.45-0.50 mm. long. Since the proglottids are attached by their full width the segmentation is not distinct.

The genital pore is marginal, situated within the first one-third or one-fourth of the proglottid. Its position alternates irregularly. The cirrus-pouch is about 0.265 mm. long by 0.105 mm. broad. The ductus ejaculatorius forms numerous coils within the cirrus-pouch. The cirrus is slender and not strongly muscular. It was not seen protruded. Testes numbering about 100 are situated in the whole dorsal field between the vitellaria. The coils of vas deferens could not be seen. The vitellaria are lateral and the follicles seem to be scattered much as in *Monticellia coryphicephala*. It was not difficult to determine that the bilobed ovary is situated in the posterior part of the proglottid but it was impossible to determine its true character. The vagina lies anterior or posterior (?) to the cirrus-pouch. Uterus and eggs could not be observed in this material.

It is unfortunate that it is impossible to give a more complete description than is here given. The specimens were stained with carmine which at its best, does not yield good outlines of organs in the cestodes. In this case the differentiation was poor making a careful study out of the question. Altho much to be desired it did not seem advisable on account of the extremely fragile condition of the specimens to attempt a restaining of the material, even had Professor Monticelli been willing that the attempt be made.

The study of this material has convinced the writer that this species belongs to the genus *Monticellia* La Rue. It is closely related to *M. coryphicephala* but seems to be quite distinct from that species. Without an examination of more material many points must remain in doubt.

#### MONTICELLIA MALOPTERURI (Fritsch) La Rue

[Figs. 154, 166]

1886:	<i>Taenia malopteruri</i>	Fritsch	1886:103-108
1891:	<i>Taenia malopteruri</i>	Monticelli	1891
1896:	<i>Ichthyotaenia malopteruri</i>	Riggenbach	1896:267
1911:	<i>Monticellia malopteruri</i>	La Rue	1911:474

Specific Diagnosis: Characters of genus. Length unknown. Breadth as much as 1.5 mm. Scolex fairly large, 0.45 mm. in breadth, quadrangular, bearing four prominent suckers. Rostellum (?) hemi-

spherical, armed with many small hooks. Suckers large, heavily muscled, protuberant, 0.25 mm. in diameter. Neck short, nearly broad as head. Mature proglottids nearly quadrate. Ripe proglottids broader than long, 1.46 mm. broad by 1.1 mm. long. Genital organs as in genus. Genital pore marginal, irregularly alternating, near middle of proglottid. Pore large, marked by a thickening of margin. Cirrus, when protruded, short and filiform. Cirrus-pouch short and relatively small, extending about one-fifth across proglottid breadth. No coils of ductus ejaculatorius in pouch. Vas deferens, a mass of coils extending to middle of proglottid. Testes filling up field between vitellaria, about 120 in number. Vagina posterior to cirrus-pouch. No coils of vagina anterior to ovary. Ovary a bilobed, winglike structure. Vitellaria follicular, situated in lateral fields. Uterus, a median tube with 18-20 lateral pouches. Eggs, not described.

Habitat: In the intestine of *Malopterurus electricus* (?), Egypt.

Fritsch described and figured this form in 1886 as *Taenia malopteruri*. Monticelli (1891) included this species in his group of fish cestodes. He did not describe it. Riegenbach (1896) considered this a species of *Ichthyotaenia*. La Rue (1911:474) considered this to be a species of *Monticellia*.

Fritsch's diagnosis reads: "*Taenia malopteruri*, Caput quadrangulare, acetabulis quattuor, angulariter positis robustis. Rostellum hemisphaericum, spinis obtusis vel tuberculis minimus ornatum. Collum mediocre. Aperturae genitalium marginales leviter circumvallatae. Corpus sulco profundo per medium impressum. Articuli adulti dimido fere longiores quam lati, proglottides breves, contracti. Habitat in intestino Malopteruri." The description given by Fritsch is very incomplete. However, he figures the head and a nearly ripe proglottid, stating the magnification of the same. Since this is true one can secure some size relations by measuring the organs portrayed in the drawings. In doing this care must be used because in some respects the drawings are not altogether clear, nor can one always determine the character of certain organs. Nevertheless the writer has used these measurements in the full realization that they were inaccurate but believing that they probably are correct within the limits of variation of the species. Besides the study of these drawings the description is based upon Fritsch's (1886) description.

The length is not stated. In breadth the worm may measure as much as 1.5 mm. The scolex (Fig. 154) is of fair size, 0.45 mm. in diameter. It is quadrangular and bears four prominent suckers and an hemispherical rostellum (?), armed with many small hooks. Suckers

are large, 0.25 mm. in diameter, heavily muscled, and protuberant from the angles of the head. The neck is short but nearly as broad as the head. Fritsch failed to state the proportions of the young proglottids, nor are the latter figured. Mature proglottids are nearly quadrate while ripe ones are somewhat broader than long. Ripe proglottids measure about 1.46 mm. broad by 1.1 mm. long. The genital organs are arranged according to the type of the genus. The marginal genital pore alternates from side to side. It is situated near the middle of the proglottid, is of large size and is marked by a considerable thickening of the margin. The cirrus is sometimes protruded and is then short and slender. The cirrus-pouch is relatively small and short. Its length goes into the proglottid breadth about five times. The ductus ejaculatorius forms no coils within the cirrus-pouch. The coils of the vas deferens form a knot extending from the cirrus-pouch to the middle of the proglottid. Testes are irregularly scattered between the vitellaria and the ovary. Fritsch figures about 120 of them. His drawing which is reproduced here (Fig. 166) does not show them in the mid-field. This may be explained in three ways: first, that the testes occupy only the lateral fields of the proglottid, second, that the preparation was of such a nature that the testes if present could not be seen on account of the eggs in the uterus, or third, that they were poorly stained. Without having seen the specimens on which Fritsch's description is based or specimens known to belong to the same lot or from the same host species one is unable to judge on this point. It is well, perhaps, to call attention to the fact that testes in ripe proglottids do not take the stain well nor are they easily seen through the mass of eggs in the uterus.

The vagina opens posterior to the cirrus-pouch. Whether it ever opens anterior to the pouch is not stated. There are no coils of the vagina anterior to the ovary. The ovary is bilobed, each lobe being somewhat winglike. It is in the posterior part of the proglottid. The lobes are apparently follicular at the outer ends, tho this feature could not be determined with any accuracy unless an examination of Fritsch's specimens were made. The vitellaria are long follicular masses in either lateral field. From the drawing the follicles of the vitellaria seem to be compacted rather than widely scattered as in the type of the genus. The uterus is a median tube from which, apparently, many lateral pouches arise. In the drawing by Fritsch these pouches are rather indistinct, but about 18-20 on either side can be seen with some degree of certainty. In the drawing, reproduced (Fig. 166) these structures are made more distinct than in the original. The eggs were not described by Fritsch.



The systematic position of this species is not readily determined from the data at hand. Fritsch's description leaves much to be desired and his figures are not sufficiently definite to render possible a positive determination. Nevertheless, certain features of the anatomy of the worm are so well delineated that some definite conclusions can be reached. The rounded summit of the head covered with numerous spines and the very prominent suckers which seem to be set on the surface of the head are not typical of *Proteocephalus*. Species of that genus lack spines on the head and their suckers are never as prominent as in the species under consideration. The head agrees very well with that of *Monticellia coryphicephala* Monticelli in regard to the suckers. The latter species has no spines. In the genital organs there seems, in the main, to be a good agreement with the members of the genus *Proteocephalus*. Nevertheless, a careful examination and comparison of Fritsch's figure of the proglottid (Fig. 166) with the writer's figure of *Monticellia coryphicephala* (Fig. 95) shows a certain resemblance that cannot be overlooked. In both species there is the more or less indefinitely outlined ovary made up of follicles at the outer regions. These follicles seem to be smaller in this species than in *M. coryphicephala*. The vitellaria, apparently, are not as extensive in the former as in the latter, yet they are different from those in *Proteocephalus*. The lips of the genital sinus are much more prominent in this species than in *Proteocephalus*. This character was not mentioned by Monticelli as being present in *Tetracotylus* nor has the writer noted it in his specimens.

In view of the facts above presented the writer must conclude that the species does not belong to the genus *Proteocephalus* Weinland. With some reservation this species is assigned to the genus *Monticellia* La Rue. The species is then to be known as *Monticellia malopteruri* (Fritsch) La Rue. The species of cestodes infesting the Siluridae merit much more careful study by modern methods. As yet their structure and relationships are almost unknown. The literature contains but few references to cestodes of this group. The writer has noted the descriptions of the species *Tetracampos ciliotheca* Wedl and *Marsypocephalus rectangulus* Wedl reported by Wedl (1861) from *Heterobranchus anguillaris*. The former because of its ventral genital pore, ciliated embryo and two bothria evidently belongs to the order Pseudophyllidea. The latter species may belong somewhere in the Proteocephalidae or Monticellidae but not sufficient data are given to warrant a positive determination. Wedl (1861) also reported *Scolex syndontis* from *Syndontis schal* and from *Heterobranchus anguillaris*. These specimens, likewise, cannot be definitely placed.

## DISTRIBUTION OF PROTEOCEPHALIDAE

The data upon which this section is based are meager yet it has seemed desirable to work over the available records to find out if there be any principles governing the distribution of the group, to find out the relation of the parasite to the primary hosts and perhaps to the secondary hosts. This section falls naturally into two parts: A, concerning the Proteocephalids infesting the amphibians and reptiles, and B, concerning those species which infest fish. The data under the first heading are grouped into certain tables and a discussion of the contents of the tables. The data bearing on the second heading, i. e., on the fish Proteocephalids are grouped under the following rubrics: List of cestode species with hosts and locality of finding; Distribution according to continents; Host species harboring two or more Proteocephalid species, with the distribution of the latter; Proteocephalids found in more than one host species, a discussion of each case including notes on the distribution and food habits of the hosts; Families of fish from which Proteocephalids are known and the species of the latter.

## DISTRIBUTION OF PROTEOCEPHALIDS OF AMPHIBIA AND REPTILIA

Amphibian Proteocephalids are known from but two continents, North America and Australia. These species are *Ophiotaenia filaroides* and *O. lönnbergii* for North America and *O. hylae* for Australia. The North American species are from the Caudata while the Australian species is from one of the Salientia. Reptilian Proteocephalids are known from all the continents. In North America are found *Ophiotaenia marenzelleri*, *O. grandis*, *O. perspicua*, and *O. lactea* sp. inq. In South America are found *O. calmettei*, *O. racemosa*, and *Crepidobothrium gerrardii*. In Europe a single species is known, namely *O. nattereri*. Africa, likewise, has yielded but a single species, *O. punica*. Asia including the tropical islands usually included in the Oriental region has three species, *Acanthotaenia shipleyi*, *Ophiotaenia pigmentata*, and *O. trimeresuri*. In Australia, i. e., in the Australian region which includes new Guinea, there are no species of *Ophiotaenia* from reptiles but there are four species of *Acanthotaenia* from reptiles, viz. *A. biróí*, *A. saccifera*, *A. tidswelli*, and *A. gallardí*.

To sum up this data there are species of *Ophiotaenia* from each continent, species of *Acanthotaenia* from two continents, Asia and Australia, and one species of *Crepidobothrium* from South America. As

yet none of these species are known to occur in more than one continent. The distribution of each species seems narrow. There are, however, but few records and the data are incomplete. When more records are available it may be found that some of these species may have a far wider distribution. In all the cases known the hosts are aquatic or semiaquatic animals and they feed in part at least upon animals which like themselves are aquatic or semiaquatic in their habits. It has not been possible to work over the rather scant literature on the food habits of these animals hence no data on that topic are here presented. It is to be hoped that someone may make a study of the food of these hosts and thus enable to be made a determination of the relationships of these parasites to each other and to their hosts.

An accompanying table gives the names of the parasites, their hosts and the locality of the collection. In another table the parasites have been grouped according to the order and family of the host. The latter table shows that there are Proteocephalid species from Caudate and Salientian Amphibians, from the Varanidae, a family of Lacertilian Reptiles, and from three families of Serpentes (Ophidia). These families are Boidae, Colubridae, and Viperidae. A single subfamily in each of the Boidae and Viperidae furnish hosts for Proteocephalids while in the family Colubridae one subfamily belonging to each of the three series furnishes host species. At the bottom of the table is placed a species which tho reported to have been taken from a dog is certainly not a dog cestode. Its nearest relatives, anatomically, are the Proteocephalids of snakes and particularly the Proteocephalids of the Crotalinae. It has been suggested elsewhere that the real host was probably one of the Crotalinae. Because of the small amount of data it has not seemed justifiable to draw many general conclusions in regard to these parasites.



## Hosts and Localities Reported for Proteocephalids of Amphibia and Reptilia

Cestode species	Hosts	Locality
<i>Acanthotaenia birói</i> (von Rätz)	<i>Varanus</i> sp.	New Guinea
<i>A. gallardi</i> Johnston	<i>Pseudechis porphyriacus</i> Shaw	New South Wales
	<i>P. australis</i> Gray	New South Wales
	<i>Notechis scutatus</i> Peters	New South Wales
	<i>Denisonia superba</i> Gunther	New South Wales
<i>A. saccifera</i> (von Rätz)	<i>Varanus</i> sp.	New Guinea
<i>A. shipleyi</i> von Linstow	<i>Varanus</i> ( <i>Hydrosaurus</i> ) <i>salvator</i>	Ceylon
<i>A. tidswelli</i> Johnston	<i>Varanus varius</i> Shaw	New South Wales
	<i>V. gouldii</i> Gray	Burnett River, Australia
	<i>V. bellii</i> (a variety of <i>V. varius</i> )	Burnett River, Australia
<i>Crepidobothrium gerrardii</i> (Baird)	<i>Eunectes murinus</i> Wagl.	South America
	<i>Boa constrictor</i> L.	South America
<i>Ophiotaenia calmetti</i> (Barrois)	<i>Lachesis</i> ( <i>Bothrops</i> ) <i>lanceolatus</i> L.	Martinique, West Indies
<i>O. filaroides</i> La Rue	<i>Amblystoma tigrinum</i> (Green)	São Paulo, Brazil
<i>O. grandis</i> La Rue	<i>Ancistrodon piscivorus</i> Holbr.	Nebraska and Kansas
<i>O. hylae</i> Johnston	<i>Hyla aurea</i>	Southern United States
<i>O. lactea</i> (Leidy) sp. inq.	<i>Natrix sipedon</i>	New South Wales
<i>O. lönnbergii</i> (Fuhrmann)	<i>Necturus maculosus</i>	(?) Eastern United States
<i>O. marenzelleri</i> (Barrois)	<i>Ancistrodon piscivorus</i> Holbr.	Ohio and Indiana
<i>O. nattereri</i> (Parona)	<i>Coluber</i> sp.	(?) Southern United States
<i>O. perspicua</i> La Rue	<i>Natrix rhombifer</i> Hallowell	Liguria, an Italian province
<i>O. pigmentata</i> (von Linstow)	<i>Psammodynastes pulverulentus</i> Boie	Illinois and Oklahoma
<i>O. punica</i> (Cholodkovski)	Dog (?), probably a snake	Java (Semarang)
<i>C. racemosa</i> (Rudolphi)	<i>Coluber</i> sp., <i>Ophiomorphus miliaris</i> , <i>Ophis merremii</i>	Island of Dscherba, Tunis
<i>O. trimeresurus</i> (Parona)	<i>Trimeresurus formosus</i>	Brazil
		Brazil
		Island of Mentawai, East Indies

## Families of Amphibia and Reptilia Harboring Proteocephalid Parasites

## AMPHIBIA

	Order	Caudata (Urodela)
Family Proteidae		
<i>Necturus maculosus</i> Raf.		<i>Ophiotaenia lönnbergii</i> (Fuhrmann)
Family Amblystomidae		
<i>Amblystoma tigrinum</i> (Green)		<i>Ophiotaenia filaroides</i> La Rue
	Order	Salientia (Anura)
Family Hylidae		
<i>Hyla aurea</i>		<i>Ophiotaenia hylae</i> Johnston

## REPTILIA

	Order	Squamata (Sauria)
	Suborder	Sauria (Lacertilia)
Family Varanidae		
<i>Varanus (Hydrosaurus) salvator</i>		<i>Acanthotaenia shipleyi</i> v. Linstow
<i>Varanus varius</i> Shaw		<i>Acanthotaenia tidswelli</i> Johnston
<i>Varanus gouldii</i> Gray		<i>Acanthotaenia tidswelli</i> Johnston
<i>Varanus bellii</i>		<i>Acanthotaenia tidswelli</i> Johnston
<i>Varanus</i> sp.		<i>Acanthotaenia birói</i> (von Rátz)
<i>Varanus</i> sp.		<i>Acanthotaenia saccifera</i> (von Rátz)
	Suborder	Serpentes (Ophidia)
Family Boidae		
Subfamily Boinae		
<i>Eunectes murinus</i> Wagl.		<i>Crepidobothrium gerrardii</i> (Baird)
<i>Boa constrictor</i>		<i>Crepidobothrium gerrardii</i> (Baird)
Family Colubridae		
Series A. Aglypha		
Subfamily Colubrinae		
<i>Natrix rhombifer</i> Hallowell		<i>Ophiotaenia perspicua</i> La Rue
<i>Natrix sipedon</i>		<i>Ophiotaenia lactea</i> (Leidy) sp. inq.
<i>Coluber</i> sp.		<i>Ophiotaenia nattereri</i> (Parona)
<i>Coluber</i> sp.		<i>Ophiotaenia racemosa</i> (Rudolphi)
<i>Ophiomorphus miliaris</i>		<i>Ophiotaenia racemosa</i> (Rudolphi)
<i>Ophis merremii</i>		<i>Ophiotaenia racemosa</i> (Rudolphi)
Series B. Opisthoglypha		
Subfamily Homalopsinae		
<i>Psammodynastes pulverulentus</i>		
Boie		<i>Ophiotaenia pigmentata</i> (von Linstow)
Series C. Proteroglypha		
Subfamily Elapinae		
<i>Pseudechis porphyriacus</i> Shaw		<i>Acanthotaenia gallardi</i> Johnston
<i>Pseudechis australis</i> Gray		<i>Acanthotaenia gallardi</i> Johnston
<i>Notechis scutatus</i> Peters		<i>Acanthotaenia gallardi</i> Johnston
<i>Denisonia superba</i> Gunther		<i>Acanthotaenia gallardi</i> Johnston

REPTILIA

Suborder Serpentes (Ophidia)

Family Viperidae

Subfamily Crotalinae

<i>Trimeresurus formosus</i>	<i>Ophiotaenia trimeresuri</i> (Parona)
<i>Lachesis (Bothrops) lanceolatus</i> L.	<i>Ophiotaenia calmettei</i> (Barrois)
<i>Ancistrodon piscivorus</i> Holbr.	<i>Ophiotaenia marenzelleri</i> (Barrois)
<i>Ancistrodon piscivorus</i> Holbr.	<i>Ophiotaenia grandis</i> La Rue

Host unknown, reported to have come

from a dog but probably from a snake *Ophiotaenia punica* (Cholodkovski)

PROTEOCEPHALIDS OF FISH

Hosts and Localities of Collection of Proteocephalid Species infesting Fish and the Species of Fish infested

Cestode Species	Hosts	Locality
<i>Proteocephalus agonis</i>	<i>Alosa finta</i> var. <i>lucustris</i>	Lake Como, Italy
<i>P. ambloplitis</i>	<i>Ambloplites rupestris</i>	Lake George, New York
	<i>Micropterus salmoides</i>	Lake George, New York; Walnut Lake, Mich.; Pelican Lake, Minn.
	<i>Micropterus dolomieu</i>	Lake St. Clair, Mich.; Lake Mendota, Wis.
<i>P. cernuae</i>	<i>Amia calva</i>	Lake St. Clair, Mich.; Lake Erie
	<i>Acerina cernua</i>	Königsberg, Prussia; Lake Balaton, Hungary
	(?) <i>Acerina schraetzer</i>	Lake Balaton, Hungary
<i>P. cyclops</i> sp. inq.	<i>Coregonus maraena</i>	Schallsee, Germany
<i>P. dubius</i>	<i>Perca fluviatilis</i>	Lake Geneva, Switzerland
<i>P. esocis</i>	<i>Esox lucius</i>	Reval, Esthonia (a Baltic province)
<i>P. exiguus</i>	<i>Coregonus nigripinnis</i> , <i>C. prognathus</i> , <i>C. artedi</i>	Lake Michigan, near Charlevoix, Mich.
<i>P. fallax</i>	<i>Coregonus maraena</i> —( <i>fera</i> )	Lake Lucerne, Switzerland
<i>P. filicollis</i>	<i>Gasterosteus aculeatus</i>	Greifswald; Berlin; Paris; Ireland
	<i>G. pungitius</i>	Rennes; Halle; Greifswald; Reval, Esthonia; Porkhala, Finland; Upsala, Sweden.
<i>P. fossatus</i>	<i>Pimelodus pati</i>	Rio Paraguay, S. A.
<i>P. hemisphericus</i> sp. inq.	<i>Anguilla vulgaris</i>	Padua, Italy
<i>P. longicollis</i>	<i>Coregonus wartmanni</i>	?
	<i>C. wartmanni nobilis</i>	Lake Lucerne



Cestode Species	Hosts	Locality
<i>P. longicollis</i>	<i>C. maraena</i> =( <i>C. lavaretus</i> and <i>C. fera</i> )	Greifswald; Rositten, E. Prussia; Lake Geneva
	<i>C. maraenula</i>	Berlin
	<i>C. albula</i>	Nikolaiken, E. Prussia
	<i>C. schinzii helveticus</i>	Lake Lucerne
	<i>C. exiguus albellus</i>	Lake Lucerne
	<i>Osmerus eperlanus</i>	Berlin; locality not recorded sev- eral times
	<i>Trutta trutta</i>	Germany (?)
	<i>T. fario</i>	?
	<i>Salmo thymallus</i>	?
	<i>S. salvelinus</i> = <i>S. alpinus</i> and <i>S. umbla</i>	Lake Lucerne; Lake Geneva; lo- cality not stated
	Very doubtful hosts!!!!	
	(?) <i>Esox lucius</i>	Lake Lucerne; Lake Balaton, Hungary
	(?) <i>Perca fluviatilis</i>	Lake Lucerne
	(?) <i>Alburnus lucidus</i>	Lake Lucerne
	(?) <i>Squalius cephalus</i>	Lake Lucerne
	(?) <i>Leuciscus leuciscus</i>	Lake Lucerne
<i>P. macrocephalus</i>	<i>Anguilla vulgaris</i>	Greifswald; Memel, East Prussia; Rennes; Padua; Narenta; Trieste; Lake Lucerne; Finland
	<i>Anguilla chrysypa</i>	Wood's Hole, Mass.; Sebago Lake, Maine
<i>P. macrophallus</i> sp. inq.	<i>Cichla monoculus</i> Spix	Brazil
<i>P. neglectus</i>	"Forelle", <i>Trutta fario</i>	Lake Lucerne and Lake Geneva, probably
<i>P. nematosoma</i> sp. inq.	<i>Esox reticulatus</i>	Locality not known, probably eastern United States
<i>P. osculatus</i> sp. inq.	<i>Silurus glanis</i>	Magdeburg and Greifswald
<i>P. pentastoma</i>	<i>Polypterus bichir</i>	Khor Attar on White Nile
<i>P. percae</i>	<i>Perca norvegica</i>	?
	<i>Perca fluviatilis</i>	Greifswald; Rositten, East Prus- sia; Finland; Upsala
<i>P. perplexus</i>	<i>Coregonus maraena</i> =( <i>C.</i> <i>lavaretus</i> )	Finland
	(?) <i>Acerina cernua</i>	?
	(?) <i>Cottus quadricornis</i>	Finland
	(?) <i>Gasterosteus aculeatus</i>	Rositten, East Prussia
	<i>Ania calva</i> and <i>Lepisosteus</i> <i>platostomus</i>	Illinois River, Havana, Illinois

Cestode Species	Hosts	Locality
<i>P. pinguis</i>	<i>Esox reticulatus</i> <i>Esox lucius</i>	Sebago Lake, Maine Walnut Lake, Michigan Lake Geneva, Wisconsin
<i>P. pusillus</i>	<i>Salmo sebago</i> <i>Cristivomer namaycush</i>	Sebago Lake, Maine Lake Temagami, Ontario
<i>Proteocephalus sagittus</i> sp. inq.	<i>Cobitis barbatula</i>	Petersburg and Province of Novgorod, Russia
<i>P. salmonis-umblae</i> sp. inq.	<i>Salmo salvelinus</i> =( <i>S. umbla</i> )	Lake Geneva, Switzerland, Germany
<i>P. salvelini</i> sp. inq.	<i>Cristivomer namaycush</i>	Outer Island, Lake Superior
<i>P. singularis</i>	<i>Lepisosteus platostomus</i>	Illinois River, Havana, Ill.
<i>P. skorikowi</i>	<i>Acipenser stellatus</i>	River Gürgen, Caspian Sea
<i>P. sulcatus</i>	<i>Polypterus endlicheri</i> <i>Claroetes laticeps</i>	Duem on the White Nile Khartoum on the White Nile
<i>P. torulosus</i>	<i>Idus melanotus</i> =( <i>Cyprinus jesus</i> and <i>Leuciscus idus</i> ) <i>Leuciscus leuciscus</i> =( <i>Squalius leuciscus</i> ) <i>L. grislagine</i> <i>Alburnus bipunctatus</i> <i>A. sp.</i> <i>A. lucidus</i> <i>Aspius rapax</i> <i>Abramis brama</i> <i>Pelecus cultratus</i> <i>Gobio fluviatilis</i> <i>Blicca bjoerkna</i> Very doubtful hosts!!!! (?) <i>Coregonus maraena</i> ( <i>fera</i> ) (?) <i>C. exiguus albellus</i> (?) <i>C. schinzii helveticus</i> (?) <i>Salmo salvelinus</i> (?) <i>Perca fluviatilis</i> (?) <i>Lota vulgaris</i>	Berlin; Greifswald; Finland Germany (?); Podiebrad, Bohemia; Lake Lucerne Locality (?) ? (Material in M. C. V.) Germany (?) (from context of report) Lakes Geneva and Lucerne Germany (?) (from context of report) Germany (?) (from context of report) Lake Balaton, Hungary Lake Balaton, Hungary Lake Lucerne Lake Lucerne Lake Lucerne Lake Lucerne and Podiebrad, Bohemia Lake Geneva
<i>Corallobothrium solidum</i>	<i>Malopterurus electricus</i>	Egypt
<i>C. lobosum</i>	<i>Silurus</i> sp.	Rio Paraguay, South America
<i>Choanoscolex abscisa</i>	<i>Silurus</i> sp.	Rio Paraguay, South America

### DISTRIBUTION OF THE PROTEOCEPHALIDS OF FISH ACCORDING TO CONTINENTS

The accompanying table lists the Proteocephalid species which are found on each continent. An examination of the table shows that in Europe there are 12 well known and 5 doubtful species. All are peculiar to Europe with the exception of *P. macrocephalus* which occurs also in North America along the Atlantic coast. In North America 9 species are known. Of these 2 are doubtful. All are peculiar except *P. macrocephalus*. From South America 4 species are recorded. All are peculiar. Likewise from Africa 3 species are recorded and all are peculiar. No species of this group have yet been reported from Asia or Australia, probably because but little parasitological work has been done on the fish of those continents. Nor are there any records as yet from the West or East Indies, Greenland, or Iceland. There has been but a single collection record from Great Britain, where the parasites of fresh-water fishes seem to have had little attention.

The records are as yet too meager to justify any broad conclusions as to the distribution of these cestodes over the larger land areas. One may expect to find the same Proteocephalid species in the hosts which are common to Europe and North America. One such case is known, namely, that of *P. macrocephalus* in *Anguilla*. *Esox lucius* which is common to both of these continents harbors one species in Europe and another one in North America. Other fish species occurring in both continents have apparently yielded no records in the literature.

Distribution of Fish Proteocephalids according to Continents

Continent	Species of Proteocephalid found
Europe	<i>Proteocephalus agonis</i> , <i>P. cernuae</i> , <i>P. cyclops</i> sp. inq., <i>P. dubius</i> , <i>P. esocis</i> , <i>P. fallax</i> , <i>P. filicollis</i> , <i>P. hemisphericus</i> sp. inq., <i>P. longicollis</i> , <i>P. macrocephalus</i> , <i>P. neglectus</i> , <i>P. osculatus</i> sp. inq., <i>P. percae</i> , <i>P. sagittus</i> sp. inq., <i>P. salmonis-umblae</i> sp. inq., <i>P. skorikowi</i> , <i>P. torulosus</i> .
North America	<i>P. ambloplitis</i> , <i>P. exiguus</i> , <i>P. macrocephalus</i> , <i>P. nematosoma</i> sp. inq., <i>P. perplexus</i> , <i>P. pinguis</i> , <i>P. pusillus</i> , <i>P. salvelini</i> sp. inq., <i>P. singularis</i> .
South America	<i>P. fossatus</i> , <i>P. macrophallus</i> sp. inq., <i>Corallobothrium lobosum</i> , <i>Choanoscolex abscisa</i> .
Africa	<i>P. pentastoma</i> , <i>P. sulcatus</i> , <i>Corallobothrium solidum</i> .
Asia	No species reported.
Australia	No species reported.



## FISH HARBORING TWO OR MORE PROTEOCEPHALID SPECIES

An examination of the complete list of fish Proteocephalids shows that there are fourteen host species which are reported to harbor more than one species of *Proteocephalus*. The data relating to these cases are presented in the accompanying table which names the hosts, their parasites and the distribution of the latter. A brief study of the table shows that of the fourteen host species ten are accredited with two species of *Proteocephalus* each, three with three, and one host with four. If from these numbers are deducted the instances of doubtfully identified species and the species inquirenda there follow these results: Five host species each harbor two well described *Proteocephalus* species while one host harbors three. There are then but six undoubted cases of two or more species of *Proteocephalus* occurring in the same host species.

An analysis of these six cases shows that in *Lepisosteus platostomus* the two parasitic species occur in the same locality, while in the cases of *Amia calva*, *Esox lucius*, and *Perca fluviatilis* the two parasitic species each occur in different localities. Likewise the three species of *Proteocephalus* found in *Coregonus maraena* occur each in different localities. The distribution of the parasites of *Trutta fario* is not known. One may conclude that two or more species of *Proteocephalus* may inhabit the same host species in the same locality or in different localities. The factors which determine this are not here shown.

Species of Fish which harbor More than One species of *Proteocephalus*

Host	<i>Proteocephalus</i> species harbored	Distribution of latter
<i>Amia calva</i>	<i>Proteocephalus perplexus</i> <i>P. ambloplitis</i>	Illinois River Lake St. Clair; Lake Erie
<i>Lepisosteus platostomus</i>	<i>P. singularis</i> <i>P. perplexus</i>	Illinois River Illinois River
<i>Salmo salvelinus</i>	<i>P. longicollis</i> <i>P. salmonis-umblae</i> sp. inq. <i>P. torulosus</i> (?)	Lakes Geneva and Lucerne, and locality not known Lake Geneva; Germany Lake Lucerne
<i>Trutta fario</i>	<i>P. longicollis</i> <i>P. neglectus</i>	Locality not known Lake Geneva and Lake Lucerne
<i>Cristivomer namaycush</i>	<i>P. pusillus</i> <i>P. salvelini</i> sp. inq.	Lake Temagami, Ontario Lake Superior

Species of Fish which harbor More than One species of *Proteocephalus* (Continued)

Host	<i>Proteocephalus</i> species harbored	Distribution of latter
<i>Coregonus maraena</i> ( <i>C. lavaretus</i> and <i>C. fera</i> )	<i>P. longicollis</i>	Greifswald; Rositten, East Prussia; Lake Geneva
	<i>P. fallax</i>	Lake Lucerne
	<i>P. percae</i>	Finland
	<i>P. torulosus</i> (?)	Lake Lucerne
<i>Alburnus lucidus</i>	<i>P. torulosus</i>	Germany (?); Lake Lucerne and Lake Geneva
<i>Leuciscus leuciscus</i>	<i>P. longicollis</i> (?)	Lake Lucerne
	<i>P. torulosus</i>	Germany (?); Bohemia; Lake Lucerne
<i>Anguilla vulgaris</i>	<i>P. longicollis</i> (?)	Lake Lucerne
	<i>P. macrocephalus</i>	Finland; Germany; France; Switzerland; Hungary; Italy (Padua)
<i>Esox lucius</i>	<i>P. hemisphericus</i> sp. inq.	Padua, Italy
	<i>P. esocis</i>	Finland
	<i>P. pinguis</i>	Maine; Michigan; Wisconsin
	<i>P. longicollis</i> (?)	Lake Lucerne; Lake Balaton, Hungary
<i>Esox reticulatus</i>	<i>P. pinguis</i>	Sebago Lake, Maine
	<i>P. nematosoma</i> sp. inq.	Eastern (?) United States
<i>Gasterosteus aculeatus</i>	<i>P. filicollis</i>	Greifswald and Berlin, Germany; Paris; Ireland
<i>Perca fluviatilis</i>	<i>P. percae</i> (?)	East Prussia
	<i>P. percae</i>	Germany; Finland; Sweden
	<i>P. dubius</i>	Lake Geneva
	<i>P. longicollis</i> (?)	Lake Lucerne
<i>Acerina cernua</i>	<i>P. cernuae</i>	Prussia; Lake Balaton, Hungary
	<i>P. percae</i> (?)	Locality unknown

## PROTEOCEPHALIDS OCCURRING IN TWO OR MORE SPECIES OF FISH

Twelve *Proteocephalid* species have been found to occur in more than one host of more or less close relationship. These species are as follows: *Proteocephalus ambloplitis*, *P. cernuae*, *P. exiguus*, *P. filicollis*, *P. longicollis*, *P. macrocephalus*, *P. percae*, *P. perplexus*, *P. pinguis*, *P. pusillus*, *P. sulcatus*, *P. torulosus*. In the following pages each of these species is discussed separately. The hosts have been investigated as to distribution and as to food habits in the hope that some clue might be found to the relations existing between host and parasite, a relation

which in some cases is far different from that expected if the idea of the specificity of hosts be strictly adhered to. The data on distribution and food habits of the hosts have been abstracted and combined from several sources, chief of which are Nitsche (1909), Leunis (1883), Bridge (1904) and Boulenger (1904) in Cambridge Natural History, volume VII, Jordan and Evermann (1896-1900), and Forbes and Richardson (1909).

*Proteocephalus ambloplitis*

This species is known at present only from waters which drain into the St. Lawrence and the Red River of the North. Altho Professor Ward examined the proper host species from the Illinois River at Havana, Ill., during the summer of 1909 his collections show that this parasite was not present there. The reported hosts are *Ambloplitis rupestris*, *Micropterus salmoides*, *M. dolomieu*, and *Amia calva*. The first three hosts have much the same distribution over eastern and central North America to the Gulf of Mexico, while *Amia calva* occurs over a somewhat more restricted area. It is abundant, however, over a large part of the area in which the other hosts are found. In many localities two, three, or even four of the hosts live in the same waters. All four hosts are carnivorous, eating other fish and crawfish. Some of them eat other food in addition. These four hosts live in the same general region, frequently in the same waters, and have certain food habits in common. Such are the conditions to be expected if the hosts are to harbor a common parasitic species. One question remaining to be solved is this: why is this species not found in the Illinois River where these hosts live in large numbers? Since the Illinois River was connected with the Great Lakes in the recent geological period the failure to find this species in this river seems the more remarkable.

*Proteocephalus cernuae*

*P. cernuae* is known at present only from Prussia and from Lake Balaton, Hungary. The waters of Prussia drain to the Baltic Sea while those of Lake Balaton drain into the Danube and so to the Black Sea. The hosts of this species are *Acerina cernua* and *A. schraetzer*. The former has a wide distribution in north and central Europe and is also found in the Danube. *A. schraetzer* is confined to the Danube and its tributaries. Thus in the Danube the ranges of the two species overlap. Both species are carnivorous and both take bottom fauna. Under these conditions of distribution and food habits one would expect to find both species harboring the same cestode species. With further study of the collections this parasite will probably be found to have a much wider and a continuous distribution.



*Proteocephalus exiguus*

*P. exiguus* has been found only in the Great Lakes. Its hosts, *Coregonus* (*Argyrosomus*) *artedi*, *C. nigripinnis*, and *C. prognathus* are all found in certain of the Great Lakes. *C. artedi* is in all the Great Lakes and neighboring waters, and north to the Arctic regions, exclusive of Alaska. *C. nigripinnis* is found in the small lakes of Wisconsin and Minnesota and in Lake Michigan. *C. prognathus* occurs probably in all the Great Lakes in deep water. Thus in Lake Michigan, at least, these species are all found. As to food habits but few data may be found for *C. prognathus* and *C. nigripinnis*. *C. artedi* feeds on Entomostraca, small molluscs and crustaceans, with larvae of insects and other animal forms including bottom fauna and spawn of the common white fish. It seems probable that the other species take many of these same food elements. Under these conditions the finding of this species in three closely related hosts is not remarkable but is to be expected.

*Proteocephalus filicollis*

This species is known only from the lower reaches of the streams flowing into the Baltic Sea, into the North Sea and the waters adjacent thereto. It apparently does not occur in the Alpine lakes. Its hosts are *Gasterosteus aculeatus* and *G. pungitius*. The latter is found all over north Europe (not in south Germany) and in North America as far southward as the Great Lakes region. *G. aculeatus* has a more restricted distribution being confined to the fresh and brackish or saline waters of Europe with the exception of the Danube drainage system. Thus the two species occupy north Europe in common. In food habits the species are much alike. Both are voracious plankton feeders; both take also fish-eggs and fry, and bottom fauna. These are the conditions which one would expect to find if the two species harbor the same parasite species. Specimens of *G. pungitius* from North America should be examined in order to learn whether they harbor the same species of parasite as the European specimens.

*Proteocephalus longicollis*

This species has a wide distribution in Germany and is known also from Switzerland. It is unknown in southern Europe, Russia or in France. It has been reported from Hungary, probably as the result of a misdetermination. Its reported hosts are mainly salmonids tho the list includes one esocid, one percoid, and three cyprinids. The accompanying table names the hosts and shows the distribution and food of each. An examination of the table shows that in a general way these

host species overlap greatly in their distribution. Several of the species occur in the same waters. Some live only in the depths of deep lakes while others live only on the surface; others live in brooks and streams, still others as *Perca fluviatilis* are ubiquitous. One host, *Trutta trutta*, lives in salt water and enters fresh water to spawn. Thus tho a species may have a wide distribution its habitat may be narrowly restricted. In the restricted habitat the food of the species is likely to be more or less restricted. Surface fish do not get the same kinds of food as do those that live on the bottom.

A survey of the table shows that all the hosts of *P. longicollis* depend on animal food tho some of them may take plant food on occasion. Certain species are much restricted as to food, so much restricted, indeed, that it may be said with some degree of certainty that some of the plankton forms must be carriers of this infection. *Coregonus wartmanni* and *C. wartmanni nobilis* are referred to as hosts which eat plankton exclusively. It is also apparent that if the records be true some other invertebrates must be carriers of the infection for several species are found which do not feed on plankton. Some molluscs may play a part as carriers. Still other fish of the list eat fish almost exclusively hence it must be that fish can serve as intermediate hosts for this parasite. It has already been shown in numerous instances that the primary host may also serve as the intermediate host for Proteocephalid species. If one considers now the different habitats and the various kinds of food taken in them it must be admitted that the evidence points toward a confusion of several species under the one name. In the opinion of the writer the validity of many of the records is doubtful. A comparative study of Proteocephalids taken from all these hosts of different localities would perhaps settle these questions as to hosts of *P. longicollis*.

Granting that all the salmonids of the list are hosts of this parasite then on the basis of food, distribution, and habitats it seems that the non-salmonids might likewise be its hosts. However, it has seemed that these records relating to the non-salmonids rest on too slender a foundation. Without an exception these records are those of Nufer (1905) whose work has been discussed in the section dealing with the description of *P. longicollis*. Parasites of these non-salmonids, especially from Lake Lucerne where Nufer was at work, ought to be subjected to a careful comparative study. This would doubtless establish or overthrow the validity of the records.

Hosts of *P. longicollis*, their Distribution and Food

Hosts	Distribution	F O O D								
		Fish	Spawn and fry	Plankton	Bottom fauna	Molluscs	Crustacea	Worms	Insect larvae	Other food
Salmonids <i>Salmo salar</i> Linnaeus = ( <i>S. alpinus</i> and <i>S. umbla</i> .)	Deep water of cold lakes of northern part of Alps; lakes of Siberia, Russia, Finland, Scandinavia, north-eastern N. America.	×		×		×				Air-borne insects
<i>Thymallus thymallus</i> L. ( <i>Salmo thymallus</i> )	Rapid streams of northern and central Europe not in lakes but in inlets and outlets. Partly migratory.		×		×	×				
<i>Trutta fario</i> L.	Clear streams, brooks, ponds, lakes of Europe especially clear mountain streams over rocky bottoms.	×					×	×	×	
<i>Trutta trutta</i> L.	North and Baltic Seas. Migrates into fresh water to spawn.									Does not feed in fresh water (?)
<i>Osmerus eperlanus</i> L.	North and Baltic Seas, also in bays and mouths of streams and in many lakes along Baltic coast.	×		×	×					
<i>Coregonus albula</i> L. ( <i>C. maraenula</i> )	Deep waters of lakes along Baltic coast, Russia to Holstein, also in Baltic sea and its arms. Migratory.			×		×		×		
<i>Coregonus maraenula</i> L. ( <i>C. lavaretus</i> and <i>C. fera</i> )	At bottom of deep large lakes of Alps, some deep lakes along Baltic coast; Baltic Sea and in certain Bavarian lakes.	×		×	×	×	×			
<i>Coregonus wartmanni</i> L.	Deep waters of large lakes on north side of Alps.			×						





*Proteocephalus macrocephalus*

This species has the widest distribution of any known *Proteocephalid*. It has been taken in many localities of northern, central and southern Europe and from two localities in eastern North America. Its hosts are *Anguilla vulgaris* and *A. chrysypa*. The former has a wide range over most of Europe, north Africa and temperate Asia. It is lacking in the Black and Caspian Seas. By some authorities this species is thought to be found also in North America. Others, including Jordan and Evermann (1896-1900) make the American form a separate species, calling it *A. chrysypa*. This species occurs over the most of North America east of the Rocky Mountains, including Mexico and the West Indies. The food habits of the two species are alike. They are voracious, and act as scavengers, preferring dead fish or other animal refuse. In view of their close relations and their similar habits it is not surprising that these species harbor the same species of parasite.

*Proteocephalus percae*

The geographical distribution of this species is imperfectly known. Up to the present time it has been taken only in East Prussia, Finland and Sweden. It has not yet been reported from the Swiss lakes tho two of its host species are abundant in that region. These hosts are *Perca fluviatilis* and *Coregonus maraena (fera)*. The appended table gives the data as to hosts, their distribution and food habits. An examination of the table shows certain points of interest. *Perca marina* which Müller gave as a host of this parasite is little known, nor is *Perca norvegica* which Rudolphi said was the host of Müller's parasite. The remaining host species overlap in their distribution. Likewise their food habits overlap to a certain extent. All eat bottom fauna tho *Perca fluviatilis* preys more on other fishes than do the other hosts. The food habits of *P. fluviatilis* and *Coregonus maraena* show close resemblance. These two species are known to harbor the species which Schneider (1905) describes as *Ichthyotaenia percae* (Müller). *Acerina cernua* and *Gasterosteus aculeatus* may harbor this parasite but it seems doubtful. These two species are known to harbor *Proteocephalus cernuae* and *P. filicollis* respectively. It seems that there may have been a mis-determination. The parasites of these two hosts and of *Cottus quadricornis* should be subjected to a re-examination.

Hosts of *Proteocephalus percae*, their Food and Distribution

Host species	Distribution	Food habits
<i>Perca norvegica</i> = <i>Perca marina</i>	No data	No data
<i>Perca fluviatilis</i>	Lakes and rivers of all Europe and northern Asia	Carnivorous, eats fish (largely species of <i>Alburnus</i> ), amphibia, snails, insects and worms
<i>Coregonus maraena</i> =( <i>C. lavaretus</i> and <i>C. fera</i> )	In deep water of large lakes of Alps, Bavaria, and near Baltic coast; Baltic Sea	Small fish, bottom fauna, Plankton, small crustacea and molluscs
<i>Acerina cernua</i>	In brackish and fresh waters of north and central Europe to Siberia; in Danube. Prefers deep water with sandy bottom	Fish eggs and fry, bottom fauna, rooting in the bottom for last
<i>Gasterosteus aculeatus</i>	In fresh and brackish or salt water of all Europe except Danube	A plankton feeder; eats fish-eggs and fry, also bottom fauna
<i>Cottus quadricornis</i>	Arctic regions south to Baltic Sea, westward to Greenland	No data on food. A close relative, <i>C. gobio</i> , eats molluscs and spawn.

*Proteocephalus perplexus*

This species is known at present only from the Illinois River at Havana, Ill. Leidy's notice (1886) of *Taenia filicollis* found in *Amia calva* from North Carolina may refer to this species. The hosts are *Amia calva* and *Lepisosteus platostomus*. The former is common in rivers and lakes of central and southern North America, including lakes Huron and Erie. The latter host, *Lepisosteus platostomus*, occurs throughout the Mississippi valley but is said to avoid the smaller streams. Thus in the Mississippi valley the two hosts have a common range. *Amia* feeds on fish, crawfish and molluscs while the other host takes fish almost exclusively. If *Lepisosteus* includes *Amia* in its diet it may secure its infection from *Amia* which may perhaps serve as both primary and secondary host. On account of its armor it is not at all likely that the gar serves as food for *Amia*. It has seemed rather remarkable that this parasite was not found in *Amia calva* of the Great Lakes. A most careful examination of the material collected by Professor Ward in the course of his work on the Great Lakes has shown that it does not exist there. Likewise it seems remarkable that the other carnivorous fish of the Illinois River, such as the bass, do not have this infection. Some of these fish eat very much the same food as *Amia*.



*Proteocephalus pinguis*

*P. pinguis* is a North American species found in widely separated localities. It has been found in small lakes of Maine, Michigan and Wisconsin. It has not yet been found in the Great Lakes. Further collections may show a much wider distribution for this species. The hosts, *Esox lucius* and *E. reticulatus*, have a wide distribution. *Esox lucius* is a cosmopolitan species of the northern hemisphere, occurring in the fresh waters of Europe, Asia and North America. In North America its range is from Alaska south to the upper Mississippi valley, east of the Rockies to the Potomac. *Esox reticulatus* is common east and south of the Alleghanies to Louisiana, and Arkansas. The ranges of these hosts are common east of the Alleghanies to the Potomac river.

Both hosts are voracious carnivores, eating fish, frogs, crawfish, mice, reptiles, water birds, and larger insects. That these two host species harbor the same species of *Proteocephalus* is then not remarkable. Since, however, *Esox lucius* is common to Europe and North America one might expect to find it harboring the same species of *Proteocephalus* in both continents. Such does not seem to be the case. This fact suggests that these two species, *P. pinguis* from North America and *P. esocis* found in the European *Esox*, have arisen as varieties of the same species or that the host upon going into the new region, either Europe or North America, has acquired a new species of parasite.

*Proteocephalus pusillus*

This species occurs in Sebago Lake, Maine, and Lake Temagami Ontario. Its hosts are *Salmo sebago* and *Cristivomer namaycush*. These two salmonids live only in fresh water and their habitats overlap to a certain extent. *Salmo sebago*, according to Jordan and Evermann (1896), occurs in Sebago Lake and northward, in lakes, rarely entering streams. *Cristivomer namaycush* lives in the lakes of New York, New Hampshire and Maine and westward to the headwaters of the Columbia and north to the Arctic circle (Forbes and Richardson, 1909). Both fish are predaceous, living largely on fish. Professor Ward's records show that in Sebago Lake *Salmo sebago* was feeding on *Osmerus mordax*. Records are too meager to allow the making of any general conclusions.

*Proteocephalus sulcatus*

This species is known only from the Nile River, from two widely separated hosts, namely *Polypterus endlicheri* and *Clarotes laticeps*. The former is one of the Polypteridae, a Crossopterygian, while the latter named host is a Silurid, of the order Teleostei. Both hosts occur in the Nile. The food habits of *Polypterus endlicheri* are not well known. One species of *Polypterus* feeds on small teleosts while others

take batrachians and crustaceans in addition to the fish. This species is no doubt carnivorous in habits. The writer is unable to find anything about the food of *Clarotes laticeps*. It seems probable, however, that it is a carnivorous species as are many others of the Siluridae. That this parasite is able to find the proper conditions of life in two species as widely separated as these seems remarkable altho not more remarkable than that *Amia calva* may serve as the host of a species characteristic of the Centrarchidae. It has, however, been pointed out in the descriptive part of the work on this species that there seems to be some reason for believing that two species have been confused under the one name.

*Proteocephalus torulosus*

This species is known only from northern and central Europe, chiefly from the Baltic drainage. Its hosts are chiefly cyprinids. All the earlier reports record it only from cyprinids. During the last few years it has been reported from Salmonids, four species, and from *Perca fluviatilis* and *Lota vulgaris*. A table is appended showing the names of the hosts as reported, their distribution, and their food. As to food the data are very fragmentary and not specific yet they are of interest. An examination of the table shows that the hosts are common in the waters of the lakes and streams of central and northern Europe. Some hosts are of wide distribution, others more or less restricted. Many of these hosts occupy the same waters, some as surface dwellers, others as bottom dwellers, some in the deep lakes, others in the small streams, while still others occur in the brackish bays and inlets of the Baltic coast. Thus the habitats are quite varied.

The food taken by the host varies to a large degree with the habitat which the host prefers. Thus from the table it is found that the food habits of the hosts listed are very different. Some are exclusively plankton feeders, others feed largely on bottom fauna or bottom fauna with plankton. Still other hosts are largely eaters of fish. If the food of the two groups of hosts, cyprinids and non-cyprinids, be considered it is noted that each of the latter group takes several kinds of food. This statement applies only to those non-cyprinids the food of which is known. Each of the cyprinids, however, takes but few kinds of food. The table speaks for itself. The cyprinids of the table are chiefly feeders on bottom fauna. Plankton forms a large part of the food of three, and fish of two of these hosts. Certain elements in the food such as airborne insects, birds, plants and probably also amphibians (semi-terrestrial forms especially) do not function as intermediate hosts for *Proteocephalus* species. For this reason they need not enter into this discussion.

Hosts of *P. torulosus*, their Distribution and Food.

Hosts	Distribution	FOOD							
		Fish	Spawn and fry	Plankton	Bottom fauna*	Molluscs	Crustacea	Worms	Insect larvae
Cyprinids <i>Idus melanotus</i>	Clear pure water of rivers, lakes and bays from France to Siberia, from Lapland to the Alps. Not in British Isles.		×	×		×			×
<i>Leuciscus leuciscus</i>	Common in cold brooks and rivers, lakes and bays of north and central Europe.					×			
<i>Leuciscus grislagine</i>	Only in deep waters of Truan-, Atter-, Mond-, and Chiem-sees. For spawning goes to the inlet and outlet streams of lakes.	×							
<i>Alburnus bipunctatus</i>	In rapid streams of middle Europe; very common in southern and western Germany; limited by altitude of 700 M.				×				
<i>Alburnus sp.</i>									
<i>Alburnus lucidus</i>	In waters of all Europe north of the Alps; not in high cold mountain streams; present in brackish waters.								No data on food
<i>Aspius rapax</i>	In shallow depths of large lakes, bays and streams of eastern and central Europe; not in Switzerland, France or the Netherlands.			×					Air borne insects
<i>Abramis brama</i>	At bottom of large lakes and slowly flowing streams of central Europe.	×							
<i>Pelecus cultratus</i>	Surface fish of brackish bays and lagoons along the Baltic, Caspian and Black Seas, whence it enters the rivers.		×	×	×				Amphibia, birds Bank fauna

\*Elements not defined.



Hosts of *P. torulosus*, their Distribution and Food (Continued)

Hosts	Distribution	F O O D							
		Fish	Spawn and fry	Plankton	Bottom fauna*	Molluscs	Crustacea	Worms	Insect larvae
Cyprinids <i>Gobio fluviatilis</i>	In central Europe and central Asia; on bottom of flowing brooks over stony ground; also in brackish waters of the Gulfs of Finland and Bothnia.								
<i>Blicca bjoerkna</i>	Common gregarious fish of all streams and lakes of Central Europe up to an altitude of 600 M.; lacking in the Alpine lakes; also found in brackish water of the Baltic Sea.				×				Non-predaceous. Food of animal origin
Non-cyprinids <i>Coregonus maraena</i>	At bottom of deep large lakes of Alps, some deep lakes along the Baltic coast; Baltic Sea and certain Bavarian lakes.	×		×	×	×	×		Plants
<i>C. exiguus albellus</i>	Lake Lucerne. Limits not known.								No data on food
<i>C. schinzi helveticus</i>	Lake Lucerne. Limits not known.								No data on food
<i>Salmo salvelinus</i>	Deep water of cold lakes of northern part of Alps, lakes of Siberia, Russia, Finland Scandinavia, north-eastern North America.	×		×		×			
<i>Perca fluviatilis</i>	Lakes and rivers of all Europe and northern Asia.	×				×		×	Amphibia
<i>Lota vulgaris</i>	Fresh waters, flowing or standing, or northern Europe, Asia and America.	×	×		×				

\*Elements not defined

How can the infection of so many species of fish with this parasite be explained? For the sake of the argument it is granted that all these species are suitable hosts for this parasite. If all these species are to be infected it is necessary that some of the invertebrates included among plankton forms, bottom fauna, and molluscs must be able to serve as intermediate hosts of this parasite. The fish which become infected from eating these invertebrate hosts may likewise become self-infected and so serve as intermediate hosts. If such fish are then eaten by the predaceous fish of the list then the latter may become infected. Thus it is possible to offer explanations that will cover the whole question of the source of infection for these hosts which have such different food habits. The analysis, however, is not very convincing. The more plausible explanation is that several species of parasite are being dealt with under this one name. It seems not improbable that the parasites of the cyprinids may belong to at least two or probably three species while the non-cyprinids may or may not harbor any of these. Further investigations on the parasites of the hosts of this list should be undertaken with the view of settling some of these questions.

#### CONCLUSIONS

A careful analysis of the extensive data presented in this section shows that species of *Proteocephalus* may occur in multiple hosts in the following combinations:

- 1) A species of *Proteocephalus* may occur in different host species of the same genus. Five species are limited exclusively to various species within the same host genus.
- 2) A species may occur in the different genera of the same family. One case.
- 3) A species may occur in the members of closely allied genera, i. e. of the same order. Four cases are known.
- 4) A species may occur in families of very wide relationships, i. e. of different orders. There are two cases of which one is doubtful.

It is further shown in this section that when a species of *Proteocephalus* occurs in multiple hosts under any of the combinations above suggested the host species have a continuous distribution. The only apparent exception to this rule is in the case of *Anguilla vulgaris* of Europe and *A. chrysypa* of North America, both harboring *P. macrocephalus*. In this case, however, the exception is apparent and not real for these two forms are perhaps no more than varieties of a cosmopolitan species. Analysis of the data presented in this section also shows that in many cases of multiple hosts the food of the different host spe-

cies is alike in some or all of its elements tho the proportions of these elements may differ widely. Since the infection of the host is only accomplished through the food eaten a general statement may be made thus: *The parasitic infestation of the host is determined by the food eaten.* The character of the food is determined by the environment and largely by the habitat preferred by the host. The apparent exceptions to the above conclusion are found in those cases where a group of species acting as hosts to a single species of parasite feed on very different elements of food. In each of these cases the probability has been pointed out that there has been a confusion of species under one name. If such a confusion does not exist then there is evidence of the remarkable adaptability of the larval stages of the parasite to the life conditions of a large series of invertebrates and fish. Both of these possibilities should be investigated.

The evidence as presented in this section is not in favor of a strict adherence to the idea of the specificity of parasites. This idea certainly does not hold for any of the better known species of *Proteocephalus* for which quite a number of collection records are available, but it seems to hold for a number of species for which there are but one or two collection records and for species which are imperfectly known. To apply the idea to these cases is not justified. To break away entirely, however, from the idea of specificity of parasites would be a rash step, indeed, for certain cases have been well established which show conclusively that for certain hosts, other than those considered in this paper, certain species of parasites are specific. Such cases can only be determined by many records of collection and then are to be relied upon only after careful infection experiments have been worked out. To apply the idea of specificity of parasites without having taken these precautions is not justifiable. In working through the data on distribution of *Proteocephalus* species which have multiple hosts one notes that in many cases the range of the parasite may be greater than the range of some of its hosts. This is well illustrated by the range of *P. longicollis* which has a far wider distribution than some of the species of *Coregonus* in which it occurs. Some of these species occur in just a few lakes while *P. longicollis* is known from many localities of northern and central Europe. So also the range of *P. macrocephalus* is greater than that of either of its hosts.

An explanation for this wide distribution of the parasite may be stated thus: The parasite may have a better means of dispersal than the host. The distribution of fish *Proteocephalids* may be widened in the following ways: They are carried by the primary host which voiding feces as it wanders about scatters the eggs of the parasite that



may infect suitable intermediate hosts. The latter, vertebrates or invertebrates, may migrate or be carried by currents to farther limits. New hosts may be infected and these on their migrations may carry the infection beyond the original limits of distribution of the parasite. The introduction by man of fish into new regions is a method of widening the range of a parasite. It is suggested as a further possibility that fish-eating birds at the time of migration may carry the eggs of the parasites ingested with the fish for some distance and these eggs being discharged with the feces into the water may infect suitable intermediate hosts. This method of dispersal could be possible only if the eggs of the parasite thus eaten are capable of withstanding the vigorous digestive action of the bird. Experiments would be required to determine the value of this method.

#### FAMILIES OF FISH FROM WHICH PROTEOCEPHALIDS ARE KNOWN

The data on this subject are collected in the accompanying table. It is there shown that Proteocephalids are known from fifteen families of fish of the group Teleostomi and representing the orders Crossopterygii, Chondrostei, Holostei, and Teleostei. The writer follows the classification of Bridge (1904) and Boulenger (1904), Vol. VII, Cambridge Natural History. Of the fifteen families ten belong to the order Teleostei. The latter contains by far the larger number of fresh water fishes. Proteocephalid species are as yet unknown from the Dipnoi. A comparison of the collection records and of the accompanying table shows that certain species of parasite seem to be characteristic of certain families of fish. Those cases in which the parasite has been recorded but once or twice probably should not be considered as characteristic of their host families. Among such cases are to be mentioned the occurrence of *P. pentastoma* in the Polypteridae, *P. skorikowi* in the Acipenseridae, *P. singularis* in the Lepisosteidae, etc. There are certain species which have been recorded several times and the majority of these times from a certain family of fish. Such species are to be considered as being characteristic for the family. The species which fall in this group are: *P. longicollis* and *P. exiguus*, characteristic of Salmonidae; *P. torulosus* of the Cyprinidae; *P. macrocephalus* of Anguillidae; *P. pinguis* of the Esocidae; *P. filicollis* of Gasterosteidae; *P. ambloplitis* of Centrarchidae; *P. percae* and *P. cernuae* of the Percidae. The remaining species are too little known to justify an attempt to determine this relationship.

Families of Fish from which Proteocephalids are Known, the Species of the Latter and the Frequency of their Occurrence

Order	Family	Species of parasite	Frequency of occurrence
Crossopterygii	Polypteridae	<i>Proteocephalus sulcatus</i>	1
		<i>P. pentastoma</i>	2
Chondrostei	Acipenseridae	<i>P. skorikowi</i>	1
Holostei	Amiidae	<i>P. perplexus</i>	1
		<i>P. ambloplitis</i>	2
Teleostei	Lepisosteidae	<i>P. singularis</i>	1
		<i>P. perplexus</i>	1
	Clupeidae	<i>P. agonis</i>	1
	Salmonidae	<i>P. longicollis</i>	20 or more
		<i>P. fallax</i>	1
		<i>P. neglectus</i>	2(?)
		<i>P. pusillus</i>	2
		<i>P. exiguus</i>	3
		<i>P. percae</i>	1
		<i>P. salmonis-umblae</i> (sp. inq.)	2
		<i>P. cyclops</i> (Immature and poorly known)	1
		<i>P. salvelini</i> (Immature and poorly known)	1
		<i>P. torulosus</i> (Doubtful determination)	4
	Cyprinidae	<i>P. torulosus</i>	18 or more
		<i>P. sagittus</i> (sp. inq.)	1
		<i>P. longicollis</i> . (Doubtful determination)	3
	Siluridae	<i>P. sulcatus</i>	1
		<i>P. fossatus</i>	1
		<i>P. osculatus</i> (sp. inq.)	2
		<i>Corallobothrium solidum</i>	1
		<i>C. lobosum</i>	1
		<i>Choanoscolex abscisa</i>	1
	Anguillidae	<i>Proteocephalus macrocephalus</i>	10
		<i>P. hemisphaericus</i> (sp. inq.)	1
	Esocidae	<i>P. esocis</i>	1
		<i>P. pinguis</i>	3
		<i>P. nematosoma</i> (sp. inq.)	2
		<i>P. longicollis</i> (Doubtful determination)	1
	Gastrosteidae	<i>Proteocephalus filicollis</i>	10

Order	Family	Species of parasite	Frequency of occurrence
	Gadidae	<i>P. torulosus</i> (Doubtful de-termination)	1
	Centrarchidae	<i>P. ambloplitis</i>	4
	Percidae	<i>P. percae</i>	5
		<i>P. cernuae</i>	3
		<i>P. dubius</i>	1
		<i>P. longicollis</i> (Doubtful de-termination)	1
	Cottidae	<i>P. percae</i> (needs confirmation)	1
	Cichlidae	<i>P. macrophallus</i>	1

Frequency of occurrence in the above table has been determined by taking the sum of the number of localities from which the species has been reported (including times from same locality) or in case it occurs in more than one host in one locality the number of host species is added. Numbers are approximate.

#### LIFE HISTORY OF THE PROTEOCEPHALIDAE

Since the appearance of a previous paper by the writer (La Rue 1909) in which he reviewed the literature on this subject and in which he outlined certain feeding experiments which had for their object the solution of the problem of the life history of the cestode infesting *Amblystoma tigrinum* but little additional data have appeared on the life history of Proteocephalids. Barbieri (1909) found that Bythotrephes and Leptodora act as intermediate hosts for *Proteocephalus agonis*. So far as can be ascertained there are no other data in the recent literature of this subject. Fuhrmann (1903) outlined the life history of Proteocephalids. Several of the older investigators have mentioned the finding of plerocercoids in the livers of fish which harbored species of *Proteocephalus* in the intestine. The writer (La Rue 1909) recorded the finding of many plerocercoids in the tissues of the salamander, *Amblystoma tigrinum*, and the positive results obtained from feeding these plerocercoids to uninfected hosts. The probability was there suggested that salamanders might become infected through the eating of infected salamanders. There is at present no reason for changing this view. While making an examination of a specimen of *Natrix rhombifer* the writer found numerous encysted plerocercoids in the tissues of the alimentary tract and of the liver. Since many snakes



are accidental or intentional cannibals it is possible that the eating of one snake by another may be one method of infection. Since also this species of snake lives largely upon fish and frogs one should look to these food animals for the intermediate host of its cestodes. No available records deal with this method of infection.

From the data presented by various workers it seems probable that the life history of the Proteocephalids is essentially as follows: The eggs and some of the ripe proglottids bearing eggs are voided by the host into the water where they are eaten by an invertebrate, perhaps a worm, an insect larva, or a crustacean, or possibly the eater is a vertebrate, fish, snake or an amphibian of the same species as the host or different. If the invertebrate or vertebrate furnishes a suitable habitat for the development of the parasite the six-hooked embryo establishes itself and from it develops a plerocercoid about which the host produces a cyst. If the intermediate host be eaten by a vertebrate which furnishes a proper habitat for the adult parasite the plerocercoid when it is released by the action of the digestive juices from its intermediate host and from its cyst passes to the intestine and develops into the adult tapeworm. If the final host engulfs material containing eggs of the cestode harbored by itself or its congeners or perhaps by members of other species the host becomes infected with the plerocercoids and so it may function as a secondary as well as a primary host for its parasitic species. Cannibalism may be a means in the spread of the parasites harbored. The problems connected with the life-history of these parasites must ultimately be settled by experimental methods.

#### ORIGIN OF THE PROTEOCEPHALIDAE

This work has thrown some light on the relations of the genera and species of Proteocephalidae to one another. It is of interest to attempt to point out the probable relations of the family to other cestodes. Like many other cestodes the members of this family were once included in the great genus *Taenia*. That, however, was before the internal structures of these cestodes were well known and it seems that the basis for this classification was the apparent similarity of the suckers. It is now evident that the Proteocephalids are most closely related structurally to the cestodes of the order Tetraphyllidea. A marked agreement in the general arrangement of all the internal organs of Tetraphyllidean cestodes is to be noted. In these respects the Proteocephalids do not agree with the Cyclophyllidea. In external features alone the Proteocephalids resemble the Cyclophyllidea more than the Tetraphyllidea. This is due to the marked simplicity of the heads and suckers of the Proteocephalids and the usual hemispherical form of the suckers.

The resemblance of the heads and suckers of *Proteocephalids* to those of *Cyclophyllideans* is, however, more apparent than real. The heads of the latter group are not readily mobile. Except in those cases where a protrusible rostellum is present the heads do not change shape much. The suckers, moreover, are strongly cupped at all times and are not much moved by the muscles of the head. The heads of the *Proteocephalids* are, as the name implies, ever changing. They undergo a multitude of changes of form and appearance. The suckers may be strongly cupped when contracted or the cavity may be entirely obliterated by the stretching of the sucker. The suckers are very mobile, being capable of being pushed out, forward or backward or laterally, and retracted. This movement of the suckers adds greatly to the protean character of the head. The whole anterior part of the head may in some species be retracted within the swollen bulbous basal part of the head. In respect to the movement of the head and the action of the suckers the *Proteocephalids* resemble the other *Tetraphyllideans*.

Another point of resemblance between the *Proteocephalids* and the other *Tetraphyllideans* is the presence of a degenerate fifth sucker in many species of the two groups. In the *Cyclophyllidea* a somewhat similar appearing structure is to be found in certain species. Here it is probably a degenerate rostellum and not a degenerate fifth sucker. Structurally the *Proteocephalidae* are to be considered as being closely allied to the *Tetraphyllidea* while their relationship to the *Cyclophyllidea* is distant. The relation of the *Proteocephalidae* to the other groups of cestodes is remote. The members of the order *Tetraphyllidea* other than the *Proteocephalidae* and *Monticellidae* are characteristic parasites of marine fishes, mostly selachians. The freshwater fishes have arisen from the marine fishes and their parasites have doubtless arisen from the parasites of the marine fishes, the *Proteocephalids* coming from a *Tetraphyllidean* ancestry.

Just which fish species was responsible for the bringing of this *Proteocephalid* stock into fresh water is a matter of conjecture. Since this group of parasites is found to be parasitic in members of so many families of freshwater fish it may be inferred that some of the older and more primitive *Teleostomi*, a *Ganoid*, brought into the freshwater environment a *Tetraphyllidean* with a simple type of head and suckers, altho this simplicity may have been a later evolution. Another hypothesis is that these parasites were introduced into fresh water by representatives of several families of fish such as the *Salmonidae*, the *Gadidae*, or the *Anguillidae*. Among the *Salmonidae* certain species have acquired the permanent habit of remaining in fresh water while others enter fresh water only to breed. The species of *Anguilla* go back to salt water

to breed and hence each individual spends part of its life in a marine environment. The Gadidae are characteristic salt water fish altho the members of one genus, *Lota*, have permanently established themselves in the freshwater environment. At the present time there is no evidence to show that species of Salmonidae or of *Anguilla* at the time of their migrations introduce into freshwater parasitic species which are capable of establishing and maintaining themselves in the new environment. Ward (1910) has pointed out that *Salmo sebago*, landlocked in lakes of eastern North America, has a parasitic fauna that is characteristic of its freshwater environment. It is evident then that whatever parasites this species brought with it from its former marine environment were unable to establish themselves. This failure may have been due to a lack of proper intermediate hosts.

These considerations lead to a possible explanation which depends on the possibility that the intermediate host species (a fish or perhaps an invertebrate) of a Tetraphyllidean acquired the habit of living in brackish and finally in fresh water. The fish species which normally made this intermediate host its food may also have made this change of environment or perhaps other fish began to prey on the intermediate host. Under these conditions the parasite might have become established in the new environment. It also seems probable that new intermediate hosts might have been acquired. The acquiring of a new host depends not on the anatomical structures of the host but upon its physiological properties and upon its habits of feeding and its environment. The fact that the head and the suckers of *Proteocephalus singularis* strongly resemble these structures in certain species of other families of Tetraphyllidea is suggestive. The host, *Lepisosteus platostomus*, is moreover a primitive fish of strong carnivorous habits. The Lepisosteidae have long been established in fresh water. It is here suggested that some member of this family may have been responsible for the introduction of Proteocephalids into the fresh water environment. The Proteocephalids of amphibians and aquatic reptiles may have been acquired in the course of development from some fish-like ancestor or it is more probable that they have acquired their Proteocephalid fauna from eating intermediate hosts (invertebrates or fish) infected with larval Proteocephalids. In this connection it is of interest to note that the head of *Crepidobothrium*, found in the Boidae, is the most primitive of all the heads of Proteocephalids of amphibians and reptiles. That is to say, it is more like the heads of other Tetraphyllideans than are the heads of its congeners. The Boidae are considered to be somewhat primitive snakes.



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## EXPLANATION OF PLATES

All original drawings, unless otherwise stated, were drawn with the aid of the camera lucida or the Edinger drawing apparatus and details have been filled in at the same magnification. Drawings are uniformly arranged with the anterior end or the dorsal surface toward the upper end of the plate unless there is a statement to the contrary.

## ABBREVIATIONS USED

<i>bm</i>	Basement membrane	<i>od</i>	Oviduct
<i>ci</i>	Cirrus	<i>oot</i>	Oötype
<i>cip</i>	Cirrus-pouch	<i>ov</i>	Ovary
<i>dj</i>	Ductus ejaculatorius	<i>ooc</i>	Oöcapt
<i>def</i>	Vas deferens	<i>rs</i>	Receptaculum seminis
<i>ef</i>	Vasa efferentia	<i>sh</i>	Shell gland
<i>ep</i>	Epithelium	<i>tt</i>	Testes
<i>exa</i>	Excretory anastomosis	<i>su</i>	Suckers
<i>exd</i>	Excretory vessel, dorsal	<i>suc</i>	Sucker cavity
<i>exv</i>	Excretory vessel, ventral	<i>suf</i>	Sucker, fifth
<i>exp</i>	Excretory pore	<i>ut</i>	Uterus
<i>glc</i>	Gland cells	<i>utl</i>	Lateral uterine pouches
<i>mc</i>	Circular muscles	<i>utv</i>	Ventral uterine outpocketings
<i>mf</i>	Muscle fibers	<i>utp</i>	Uterine passage
<i>ml</i>	Longitudinal muscles	<i>utvp</i>	Ventral uterine pores
<i>mr</i>	Muscle rhomboid	<i>va</i>	Vagina
<i>ms</i>	Muscle star	<i>vas</i>	Sphincter vaginae
<i>mtr</i>	Transverse muscles	<i>vi</i>	Vitellaria
<i>mx</i>	Muscle cross	<i>vid</i>	Vitelline ducts
<i>nl</i>	Lateral nerve	<i>vidc</i>	Vitelline duct, common
<i>nr</i>	Nerve ring		

## EXPLANATION OF PLATE

Fig. 1.—*Proteocephalus macrocephalus* (Creplin), head, toto. Lot 71, Sebago Lake. Ward Collection.

Fig. 2.—*Proteocephalus pusillus* Ward, head, toto, showing fifth sucker. From *Cristivomer namaycush*, Lake Temagami.

Fig. 3.—*Proteocephalus pusillus* Ward, head, toto, showing fifth sucker. From *Salmo sebago*, Sebago Lake.

Fig. 4.—*Proteocephalus pusillus* Ward, head, toto, showing fifth sucker. From *Cristivomer namaycush*, Lake Temagami.

Fig. 5.—*Proteocephalus cernuae* (Gmelin), head, toto. From lot 09.26 Ward Collection.

Fig. 6.—*Proteocephalus cernuae* (Gmelin), head, toto. From lot 09.26 Ward Collection.

Fig. 7.—*Proteocephalus torulosus* (Batsch), head, toto, a characteristic shape.

Fig. 8.—*Proteocephalus percae* (Müller), head, toto. From lot 10.122 Ward Collection.

Fig. 9.—*Proteocephalus percae* (Müller), head, toto. From lot 10.123 Ward Collection.

Fig. 10.—*Ophiotaenia perspicua* La Rue, head, toto.

Fig. 11.—*Ophiotaenia calmettei* (Barrois), head, toto.

Fig. 12.—*Crepidobothrium gerrardii* (Baird), head, toto. From lot 08.472 Ward Collection.

Fig. 13.—*Crepidobothrium gerrardii* (Baird), head, toto. From lot 10.190 Ward Collection.

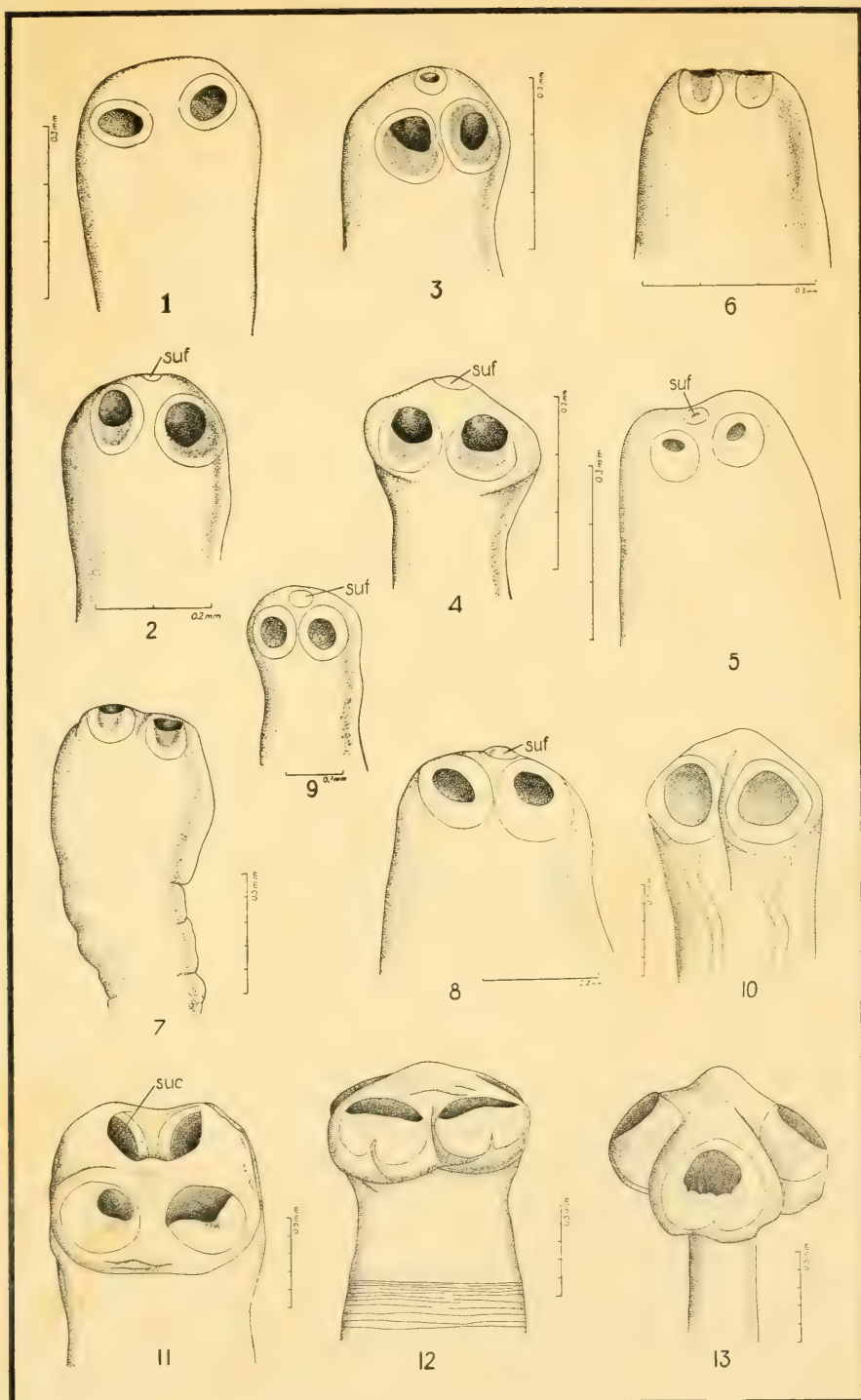


PLATE I





## PLATE II

## EXPLANATION OF PLATE

- Fig. 14.—*Proteocephalus exiguus* La Rue, head, toto.
- Fig. 15.—*Proteocephalus filicollis* (Rud). = *ambiguus* (Dujardin), head drawn from Schneider's in toto preparation.
- Fig. 16.—*Proteocephalus esocis* (Schneider), head, drawn from a specimen cleared in glycerine.
- Fig. 17.—*Proteocephalus perplexus* La Rue, head, toto.
- Fig. 18.—*Proteocephalus ambloplitis* (Leidy), head, toto. From material collected at Walnut Lake, Mich.
- Fig. 19.—*Proteocephalus ambloplitis* (Leidy), head, toto. From material collected at Walnut Lake, Mich.
- Figs. 20, 21 and 22.—*Proteocephalus dubius* La Rue, heads, toto, showing fifth sucker and contraction states of the suckers.
- Fig. 23.—*Proteocephalus fallax* La Rue, head, toto, showing fifth sucker.
- Fig. 24.—*Proteocephalus singularis* La Rue, head, toto. Apical prominence contracted.
- Fig. 25.—*Proteocephalus singularis* La Rue, head, toto. Apical prominence extended.
- Fig. 26.—*Ophiotaenia filaroides* La Rue, head of adult, toto. After La Rue 1909.
- Fig. 27.—*Ophiotaenia filaroides* La Rue, head of plerocercus, toto, showing vestigial fifth sucker after atrophy is well under way. After La Rue 1909.
- Fig. 28.—*Ophiotaenia filaroides* La Rue, head of plerocercus, toto, showing outline of hypertrophied fifth sucker. After La Rue 1909.
- Fig. 29.—*Proteocephalus pinguis* La Rue, head, toto, dorsal or ventral view.
- Fig. 30.—*Proteocephalus pinguis* La Rue, head, toto, dorsal or ventral view.
- Fig. 31.—*Proteocephalus pinguis* La Rue, head, toto, lateral view. Figs. 29, 30, and 31 are from lot 8, Sebago Lake. Ward Collection.
- Fig. 32.—*Proteocephalus pinguis* La Rue, head and regions of strobila, toto. From material collected at Walnut Lake, Mich.
- Fig. 33.—*Crepidobothrium gerrardii* (Baird), head, toto. After Smith 1908.
- Fig. 34.—*Crepidobothrium gerrardii* (Baird), head, toto. After Smith 1908.
- Figs. 35 and 36.—*Proteocephalus pinguis* La Rue, heads, toto, showing variation in contraction states. From material collected at Walnut Lake, Mich.
- Fig. 37.—*Ophiotaenia marenzelleri* (Barrois), head, toto, after Schwarz.
- Fig. 38.—*Ophiotaenia grandis* La Rue, head, toto, showing swollen region back of head.



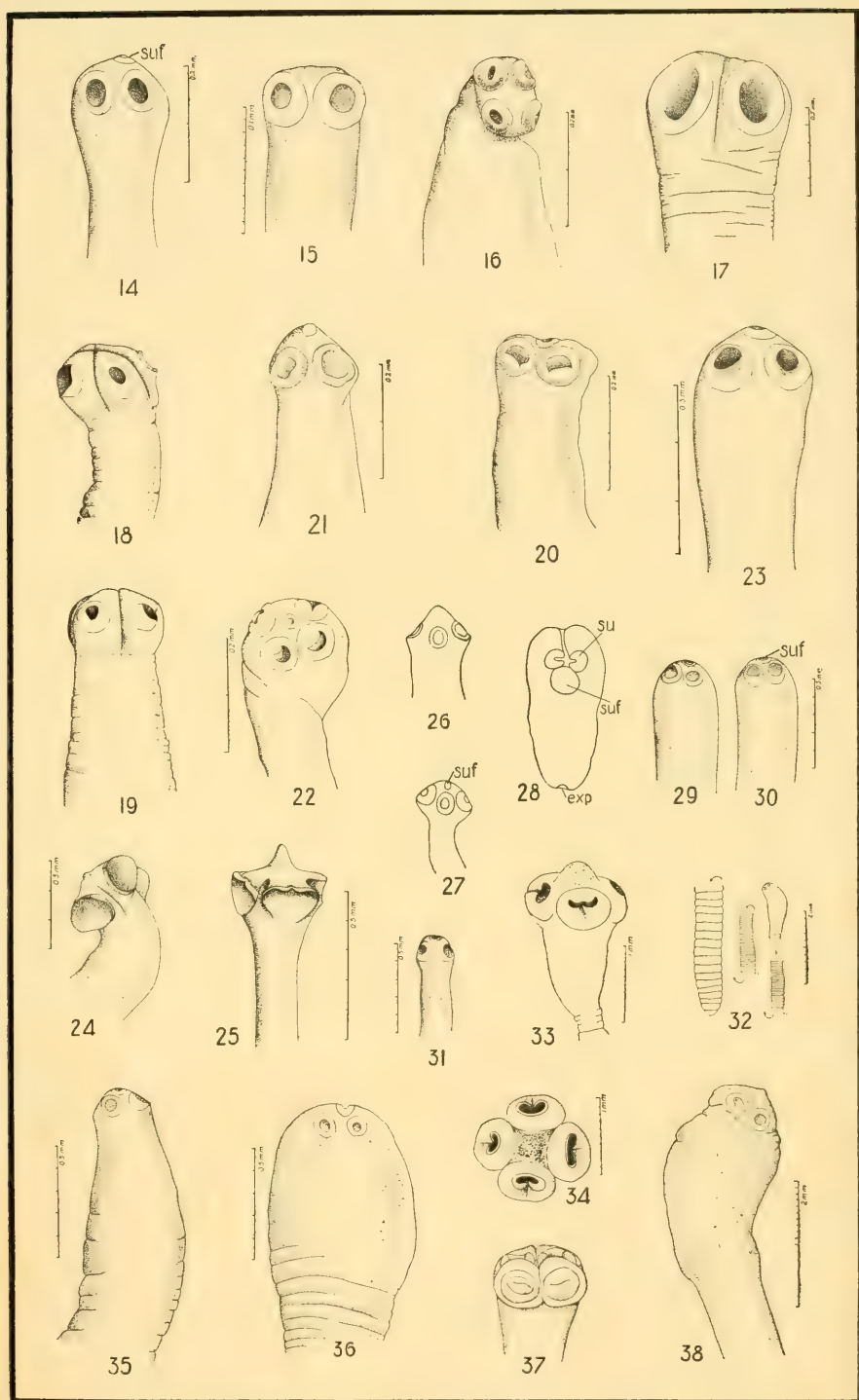


PLATE II



## PLATE III



## EXPLANATION OF PLATE

Fig. 39.—*Proteocephalus singularis* La Rue, head, cross-section about 0.10 mm. from the tip of the head, near the upper end of suckers. This section shows the beginning of the muscle cross, *mx*, and the heavy muscles connecting the sucker wall with the surface of the head. Figs. 39 and 40 are drawn to the same scale as Fig. 41.

Fig. 40.—*Proteocephalus singularis* La Rue, head, cross-section about 0.135 mm. below tip of head and about middle of suckers. Shows heavy muscle across, *mx*, with some fibers reaching out to the surface of the head between the suckers.

Fig. 41.—*Proteocephalus singularis* La Rue, head, cross-section near lower edge of suckers, showing muscle star, *ms*, with broadly flared ends. Nuclei are shown as the larger black spots. The closely packed groups of short heavy lines are tangentially cut ends of muscle fibers which attach to the suckers.

Fig. 42.—*Crepidobothrium gerrardii* (Baird), vestigial fifth sucker, cross-section. Note sucker cavity and musculature. Nuclei could not be seen in this tissue.

Fig. 43.—*Ophiotaenia filaroides* La Rue, vestigial fifth sucker, from a frontal section of a plerocercus. Note the sucker cavity filled with granules, basement membrane, nuclei and muscle fibers in and around sucker. Compare structure of vestigial sucker with that of the normal sucker beside it.

Fig. 44.—*Ophiotaenia filaroides* La Rue, vestigial fifth sucker, frontal section of head of plerocercus. Compare structures with those of Fig. 43. Scale should read 0.05 mm.

Fig. 45.—*Ophiotaenia filaroides* La Rue, vestigial fifth sucker from a cross-section of head of a plerocercus. Note the sucker cavity filled with granules, the basement membrane, the muscles, and nuclei.

Fig. 46.—*Ophiotaenia filaroides* La Rue, vestigial fifth sucker, cross-section of head of plerocercus. Note points mentioned for Fig. 45. Sucker cavity only partly filled with granules. Scale should read 0.05 mm.

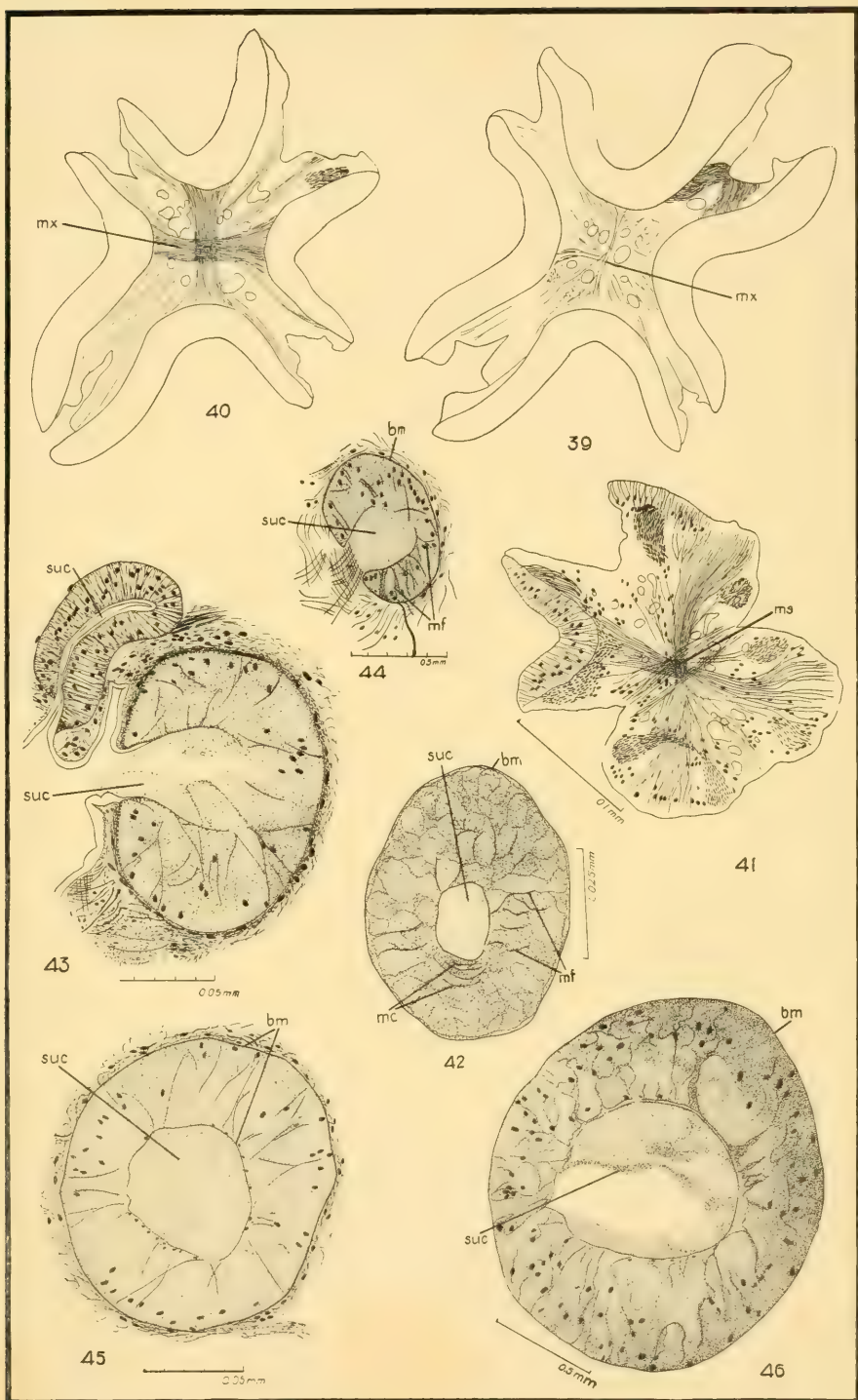


PLATE III





## PLATE IV

## EXPLANATION OF PLATE

Fig. 47.—*Proteocephalus macrocephalus* (Creplin), ripe proglottid showing female reproductive organs. From Sebago Lake material.

Fig. 48.—*Proteocephalus macrocephalus* (Creplin), ripe proglottid, cross-section in region of cirrus-pouch. Partial reconstruction. From Sebago Lake material.

Fig. 49.—*Proteocephalus macrocephalus* (Creplin), ripe proglottid showing male organs. From Sebago Lake material.

Fig. 50.—*Proteocephalus exiguus* La Rue, mature proglottid, toto.

Fig. 51.—*Proteocephalus exiguus* La Rue, end-proglottid, ventral view of toto preparation. Note the excretory pore and the shape of the ovary.

Fig. 52.—*Proteocephalus exiguus* La Rue, ripe proglottid, toto, as seen from dorsal side, testes omitted.

Fig. 53.—*Proteocephalus pusillus* Ward, ripe proglottid, toto, showing uterine pouches and a rare abnormality in the position of the vagina which is here posterior to the cirrus-pouch. From *Salmo sebago*.

Fig. 54.—*Proteocephalus pusillus* Ward, mature proglottid, toto. From *Salmo sebago*.

Fig. 55.—*Proteocephalus pusillus* Ward, mature proglottid, toto, showing male reproductive organs and the usual relation of vagina and cirrus-pouch. From *Cristivomer namaycush*.

Fig. 56.—*Proteocephalus fallax* La Rue, ripe proglottid, toto. Shows two ventral uterine pores. This figure is inverted.

Fig. 57.—*Proteocephalus fallax* La Rue, mature proglottid, toto, ventral view. Note musculature of cirrus-pouch.

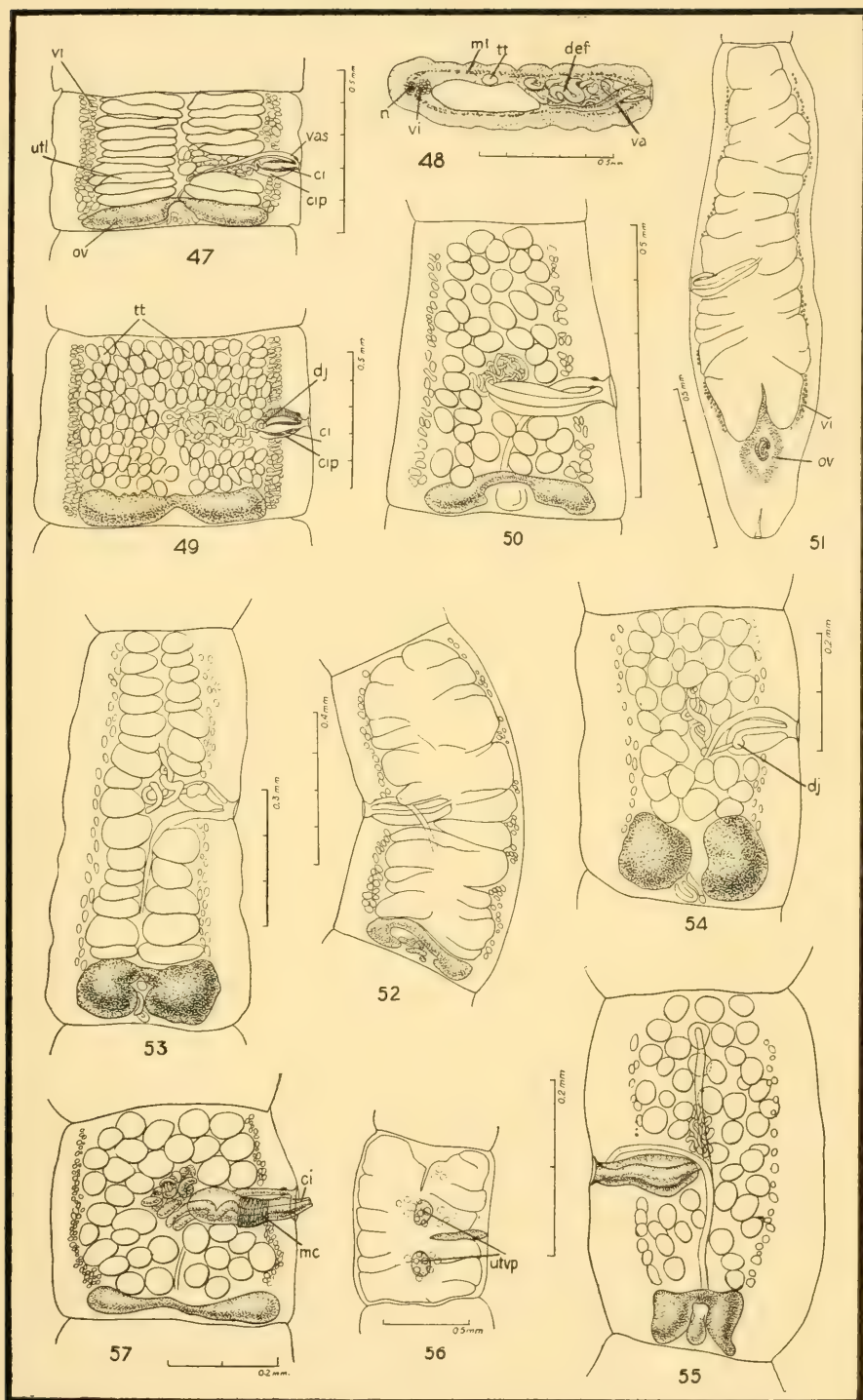


PLATE IV





## PLATE V

## EXPLANATION OF PLATE

Fig. 58.—*Proteocephalus filicollis* (Rud.)=*ambiguus* (Dujardin), whole worm. This figure and Figs. 59 and 60 were drawn from Schneider's toto preparation.

Fig. 59.—*Proteocephalus filicollis* (Rud.)=*ambiguus* (Dujardin), mature proglottid, toto.

Fig. 60.—*Proteocephalus filicollis* (Rud.)=*ambiguus* (Dujardin), ripe proglottid, toto.

Fig. 61.—*Proteocephalus esocis* (Schneider), young proglottid, toto. Vagina and cirrus-pouch could not be traced to margin of proglottid.

Fig. 62.—*Proteocephalus esocis* (Schneider), mature proglottid, toto.

Fig. 63.—*Proteocephalus esocis* (Schneider), outline of anterior end, posterior end and middle of strobila.

Fig. 64.—*Proteocephalus perplexus* La Rue, ripe proglottid, reconstruction showing female reproductive organs, especially lateral pouches of uterus.

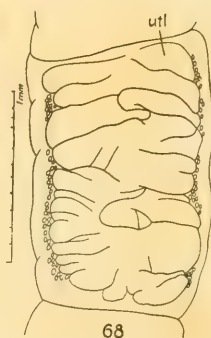
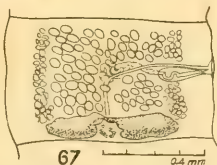
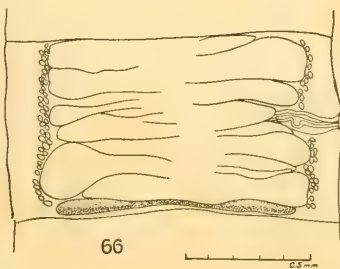
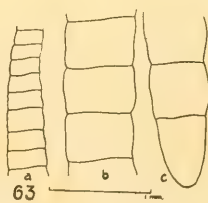
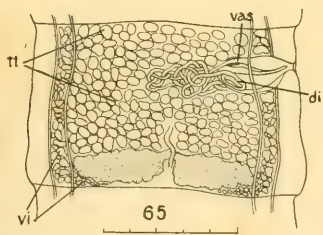
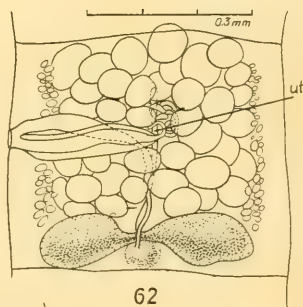
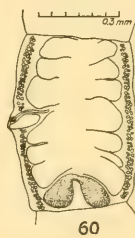
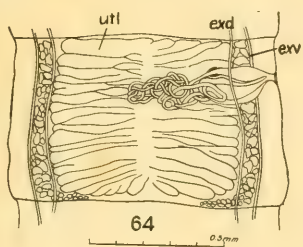
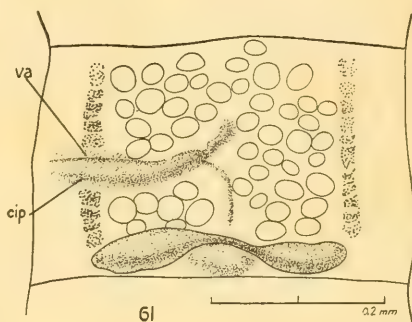
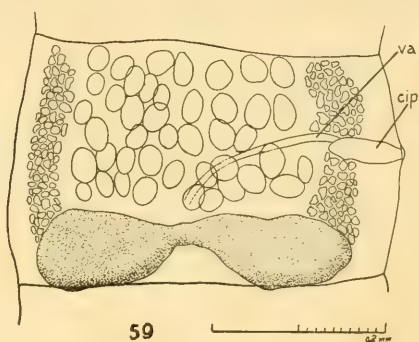
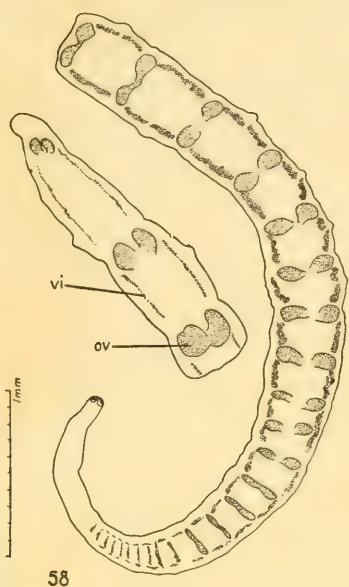
Fig. 65.—*Proteocephalus perplexus* La Rue, ripe proglottids, reconstruction showing male reproductive organs and the ovary. Note also the position of the sphincter vaginae. Figs. 64 and 65 are drawn from the same series of sections. Scale should read 0.5 mm.

Fig. 66.—*Proteocephalus cernuae* (Gmelin), ripe proglottid, toto, showing especially the uterine pouches and the slender ovarian lobes.

Fig. 67.—*Proteocephalus cernuae* (Gmelin), mature proglottid, toto.

Fig. 68.—*Proteocephalus cernuae* (Gmelin), old proglottid, toto.







## PLATE VI

## EXPLANATION OF PLATE

Fig. 69.—*Proteocephalus percae* (Müller), ripe proglottid, toto, ventral view. From one of Schneider's slides.

Fig. 70.—*Proteocephalus percae* (Müller), ripe proglottid, toto, dorsal view. Testes omitted to show uterine pouches. From one of Schneider's slides.

Fig. 71.—*Proteocephalus percae* (Müller), ripe proglottid, partial reconstruction from ventral side showing relation of reproductive organs. From lot 10.123 Ward Collection.

Fig. 72.—*Proteocephalus percae* (Müller), ripe proglottid, toto. Uterine pouches omitted. From lot 10.123 Ward Collection.

Fig. 73.—*Proteocephalus percae* (Müller), fifth sucker, section showing structure. From lot 10.122 Ward Collection.

Fig. 74.—*Proteocephalus percae* (Müller), ripe proglottid, partial reconstruction of cross-sections to show relationship of organs in region of cirrus-pouch as seen from anterior end. From lot 10.122 Ward Collection. The letters va at the extreme right of the figure should read vas.

Fig. 75.—*Proteocephalus dubius* La Rue, ripe proglottid, toto showing uterine pouches and shape of decadent ovary. Scale is in error, each unit equals 0.1 mm.

Fig. 77.—*Proteocephalus dubius* La Rue, mature proglottid, toto.



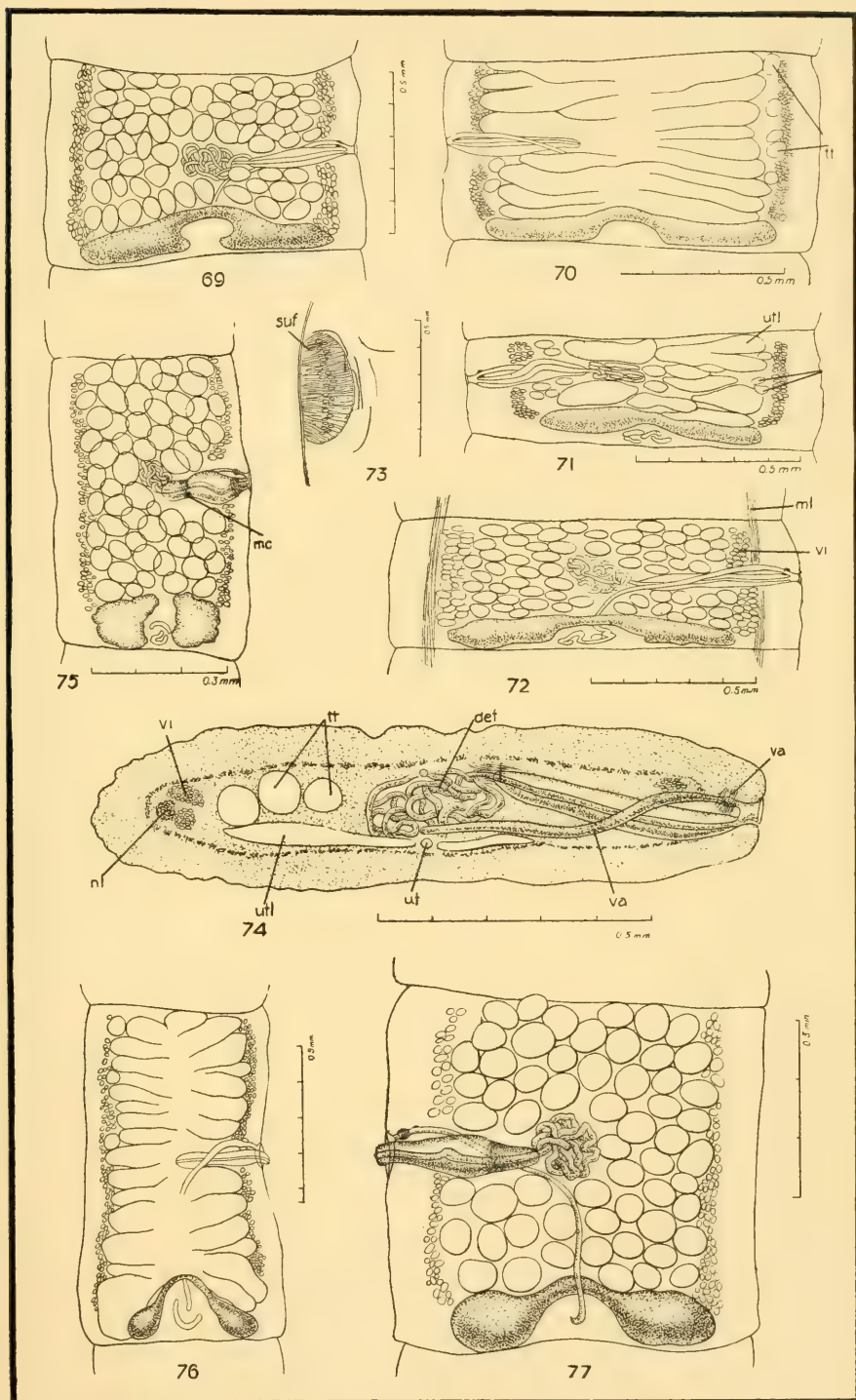


PLATE VI



## PLATE VII

## EXPLANATION OF PLATE

Fig. 78.—*Proteocephalus torulosus* (Batsch), ripe proglottid, frontal section showing small part of uterus and ovary, testes covering almost the entire area between vitellaria.

Fig. 79.—*Proteocephalus torulosus* (Batsch), ripe proglottid, frontal section showing relatively large size of ovary and the small number of uterine pouches.

Fig. 80.—*Proteocephalus torulosus* (Batsch), ripe proglottid, cross-section in region of cirrus-pouch.

Fig. 81.—*Proteocephalus neglectus* La Rue, ripe proglottids, toto, showing reproductive organs. The cirrus-pouch is much shortened, some ducts omitted. Ventral view.

Fig. 82.—*Proteocephalus neglectus* La Rue, cirrus-pouch and vagina, normal position and shape. Funnel-like atrium possibly a little exaggerated. Note the muscle fibers at end of cirrus-pouch.

Fig. 83.—*Proteocephalus singularis* La Rue, ripe proglottid, frontal section showing uterine pouches and the cut parts of the much coiled excretory ducts.

Fig. 84.—*Proteocephalus singularis* La Rue, cirrus-pouch and vagina, reconstruction. Note position of vaginal sphincter and of the dilated portion of the vagina.

Fig. 85.—*Proteocephalus singularis* La Rue, ripe proglottid, frontal section showing arrangement of testes, vitellaria and ovary. Vagina and cirrus-pouch not shown.

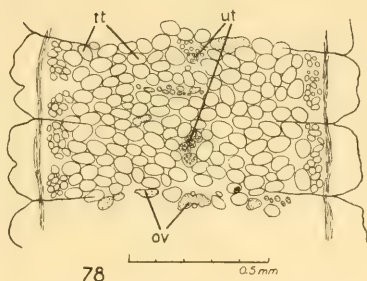
Fig. 86.—*Proteocephalus singularis* La Rue, head, frontal section showing appearance and position of transverse and longitudinal muscles.

Fig. 87.—*Proteocephalus singularis* La Rue, head, frontal section showing attachments of longitudinal muscles to the suckers. Scale should read 0.2 mm.

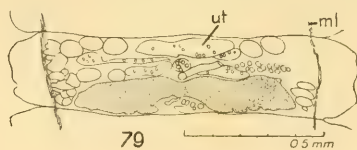
Fig. 88.—*Proteocephalus pinguis* La Rue, proglottid, portion of cross-section showing relation of vagina, cirrus-pouch and excretory ducts.

Fig. 89.—*Proteocephalus pinguis* La Rue, ventral uterine pores leading to exterior. Shown in frontal section of proglottid just below cuticula.

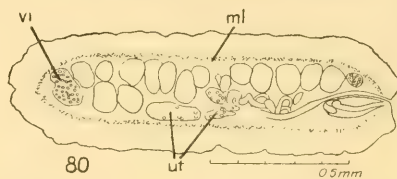




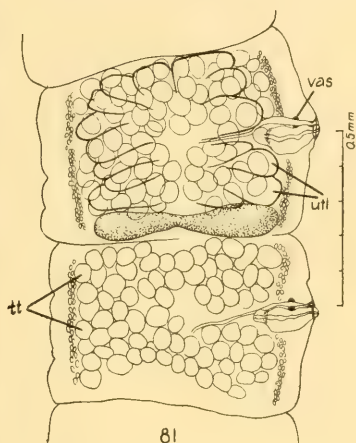
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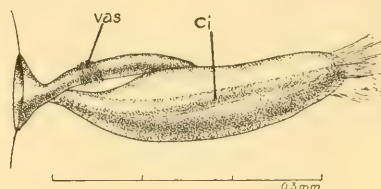
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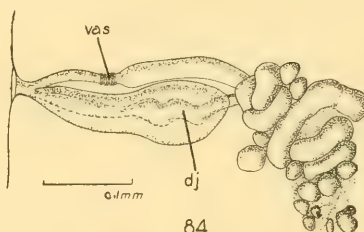
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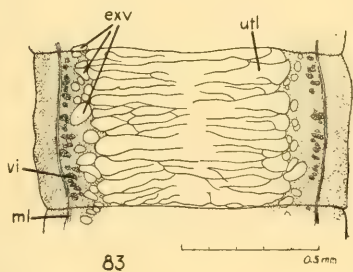
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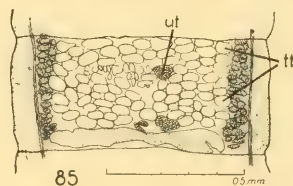
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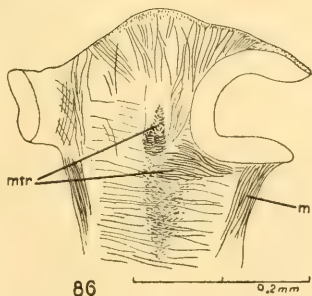
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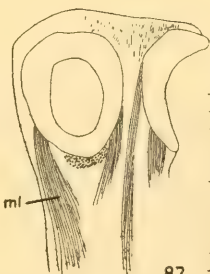
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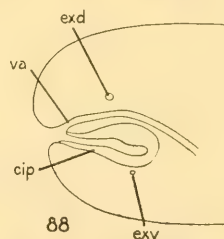
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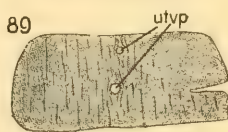
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## PLATE VIII

## EXPLANATION OF PLATE

Fig. 90.—*Proteocephalus pinguis* La Rue, cirrus, vagina, vas deferens and portion of vasa efferentia. From a reconstruction. Scale should read 0.1 mm.

Fig. 91.—*Proteocephalus pinguis* La Rue, complex of excretory ducts leading to the dorsal and ventral surfaces of the proglottid.

Fig. 92.—*Proteocephalus pinguis* La Rue, ripe proglottid, toto, ventral view. From lot 8, Sebago Lake material.

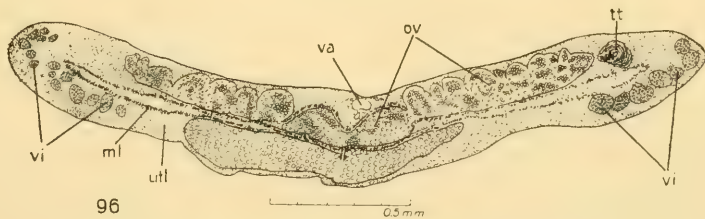
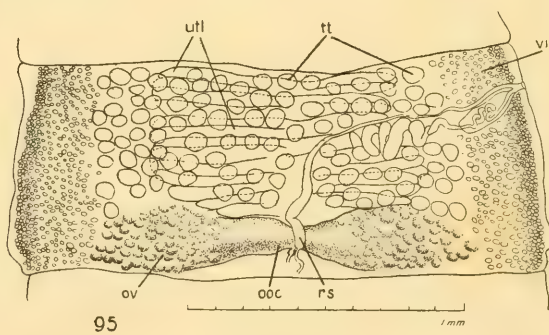
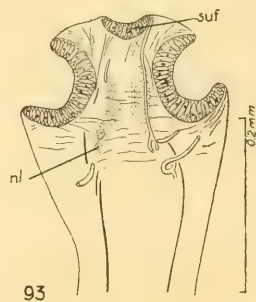
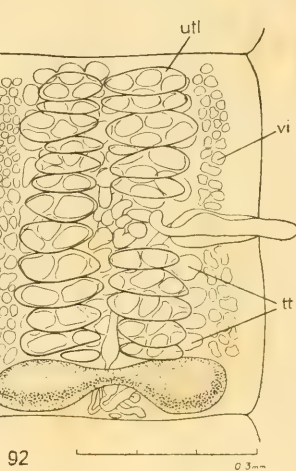
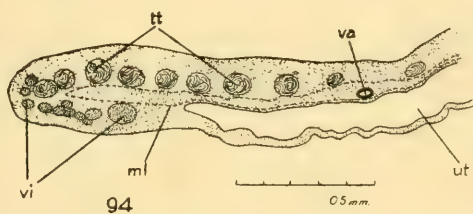
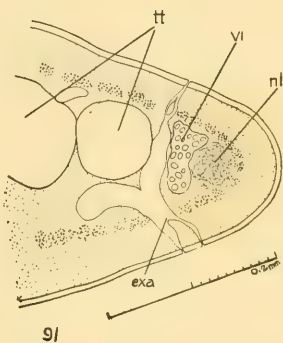
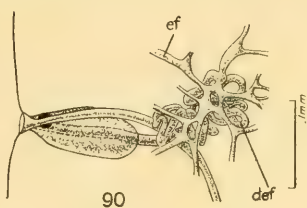
Fig. 93.—*Proteocephalus pinguis* La Rue, head, longitudinal section showing structure of suckers, etc.

Fig. 94.—*Monticellia coryphicephala* (Monticelli), ripe proglottid, cross-section showing relations of organs to the muscle-sheath. From one of Monticelli's preparations.

Fig. 95.—*Monticellia coryphicephala* (Monticelli), ripe proglottid, toto, showing peculiar appearance of ovary, distribution of testes over entire field between vitellaria, and the scattered vitelline follicles. From one of Monticelli's preparations. Cf. Fig. 186.

Fig. 96.—*Monticellia coryphicephala* (Monticelli), ripe proglottid, cross-section through region of ovary showing peculiar relation of organs to muscle-sheath. Note that the ovary is partly outside and partly inside this sheath. From one of Monticelli's preparations.







## PLATE IX

## EXPLANATION OF PLATE

Fig. 97.—*Ophiotaenia grandis* La Rue, cirrus-pouch and vagina, cirrus partly protruded.

Fig. 98.—*Ophiotaenia grandis* La Rue, cirrus-pouch and vagina, cirrus partly protruded.

Fig. 99.—*Ophiotaenia grandis* La Rue, organs of interovarial space as seen in an in toto preparation.

Fig. 100.—*Ophiotaenia grandis* La Rue, two proglottids showing indentation at the genital pore. No genital atrium visible.

Fig. 101.—*Ophiotaenia grandis* La Rue, mature proglottid, toto, ventral view showing reproductive organs and ventral uterine pores.

Fig. 102.—*Ophiotaenia perspicua* La Rue, ripe proglottid, toto showing uterine pouches.

Fig. 103.—*Ophiotaenia filaroides* La Rue, ripe proglottid, showing uterine pouches and protruded cirrus.

Fig. 104.—*Ophiotaenia filaroides* La Rue, organs of interovarial space from a reconstruction. After La Rue 1909. Through an error in lettering the lower part of the vagina is marked 'od' whereas the fertilization passage beneath the vagina should be marked 'od'. 'Ys' should read 'rs'.

Fig. 105.—*Ophiotaenia filaroides* La Rue, mature proglottid, toto, unflattened, showing relationships of organs. After La Rue 1909.



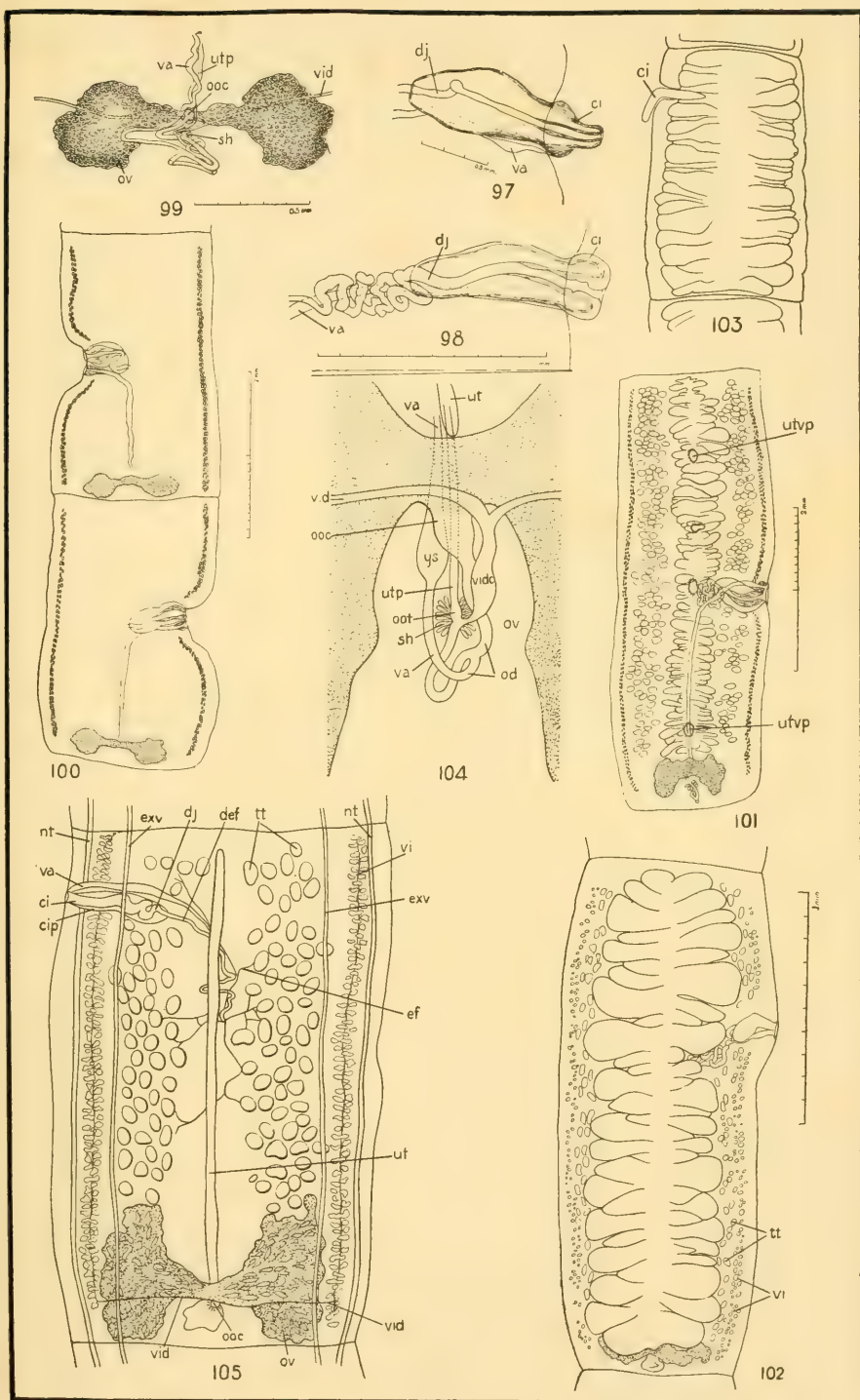


PLATE IX



## PLATE X

## EXPLANATION OF PLATE

Fig. 106.—*Ophiotaenia trimeresuri* (Parona), evaginated cirrus, cirrus-pouch and vagina. Note coils of ductus ejaculatorius in the swollen cirrus. Scale should read 0.3 mm.

Fig. 107.—*Ophiotaenia trimeresuri* (Parona), cirrus-pouch and vagina, cirrus unprotruded. Note coils of ductus ejaculatorius in the cirrus-pouch. Scale should read 0.3 mm.

Fig. 108.—*Ophiotaenia trimeresuri* (Parona), mature proglottid, toto. Uterine pouches just beginning to form.

Fig. 109.—*Ophiotaenia calmettei* (Barrois), mature proglottid, toto. Uterine pouches more advanced than in Fig. 110.

Fig. 110.—*Ophiotaenia calmettei* (Barrois), mature proglottid, toto. Beginnings of uterine pouches may be seen.

Fig. 111.—*Crepidobothrium gerrardii* (Baird), mature proglottid, toto. From lot 10.179 Ward Collection.

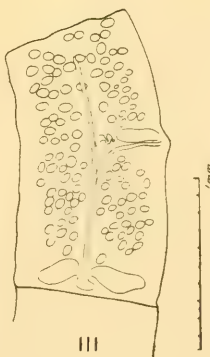
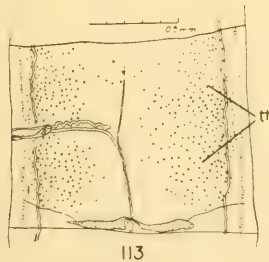
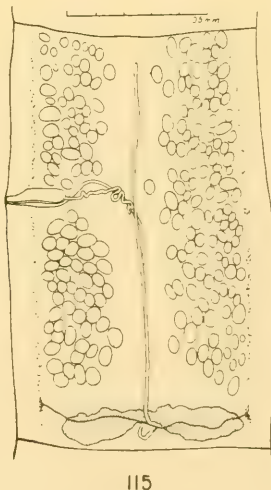
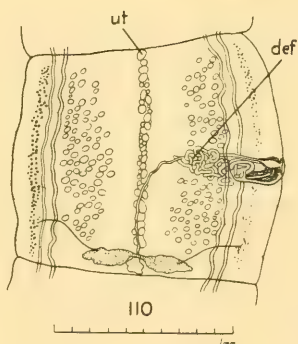
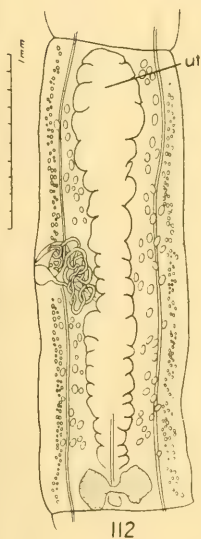
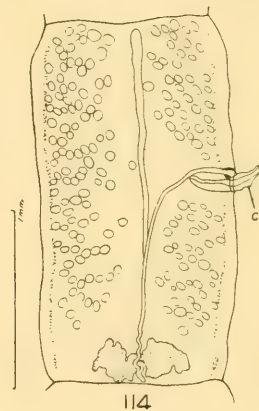
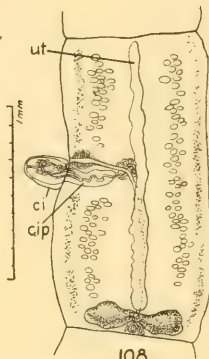
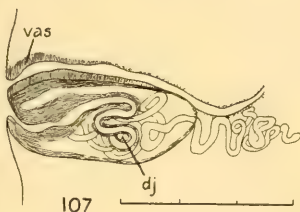
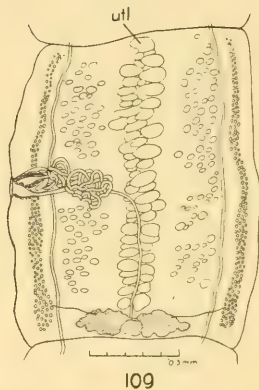
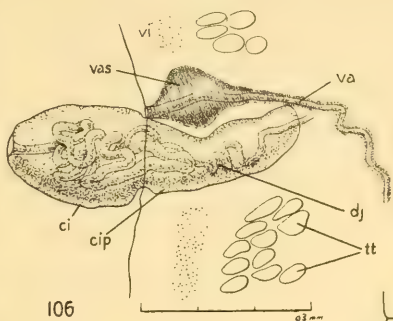
Fig. 112.—*Crepidobothrium gerrardii* (Baird), ripe proglottid, toto. From lot 08.472 Ward Collection.

Fig. 113.—*Crepidobothrium gerrardii* (Baird), nearly mature proglottid, toto. Note the great number of testes. From lot 10.190 Ward Collection.

Fig. 114.—*Crepidobothrium gerrardii* (Baird), mature proglottid, toto. Cirrus protruded. Drawn from slide No. 1858, Bureau of Animal Industry, Washington.

Fig. 115.—*Crepidobothrium gerrardii* (Baird), mature proglottid, toto.







## PLATE XI

## EXPLANATION OF PLATE

Fig. 116.—*Proteocephalus ambloplitis* (Leidy), head, frontal section showing vestigial fifth sucker. After Benedict.

Fig. 117.—*Proteocephalus ambloplitis* (Leidy), head, toto. After Benedict.

Fig. 118.—*Proteocephalus exiguus* La Rue, ripe proglottid showing arrangement of organs. After Benedict.

Fig. 119.—*Ophiotaenia lönnbergii* (Fuhrmann), head, toto. After Fuhrmann.

Fig. 120.—*Proteocephalus percae* (Müller), head, frontal section showing fifth sucker. After Schneider.

Fig. 121.—*Proteocephalus percae* (Müller), head, toto. Reproduction of Müller's figure 2.

Fig. 122.—*Proteocephalus percae* (Müller), head, toto. Reproduction of Müller's figure 3.

Fig. 123.—*Crepidobothrium gerrardii* (Baird), head, toto. After Monticelli.

Fig. 124.—*Crepidobothrium gerrardii* (Baird), head, toto. After Monticelli.

Fig. 125.—*Monticellia macrocotylea* (Monticelli), head. After Monticelli.

Fig. 126.—*Proteocephalus pentastoma* (Klaptocz), anterior face of head. After Klaptocz.

Fig. 127.—*Proteocephalus pentastoma* (Klaptocz), head and neck. After Klaptocz.

Fig. 128.—*Proteocephalus pentastoma* (Klaptocz), portion of middle of worm. After Klaptocz.

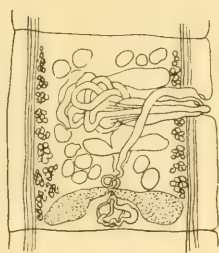
Fig. 129.—*Proteocephalus pentastoma* (Klaptocz), posterior part of worm. After Klaptocz.

Fig. 130.—*Proteocephalus sulcatus* (Klaptocz), head, anterior face. After Klaptocz.

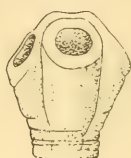
Fig. 131.—*Proteocephalus sulcatus* (Klaptocz), head. After Klaptocz.

Fig. 132.—*Monticellia coryphicephala* (Monticelli), head, toto. Note the prominence of the suckers. After Monticelli.

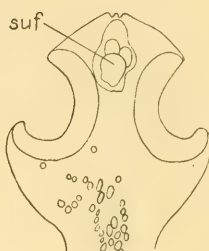




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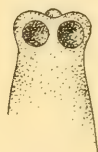
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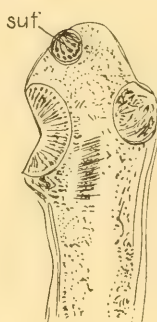
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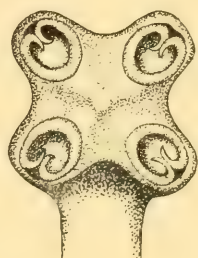
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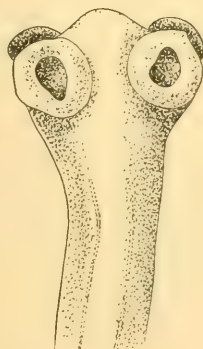
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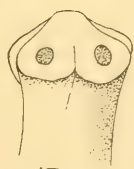
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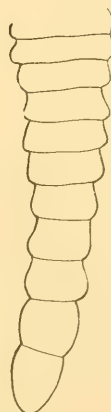
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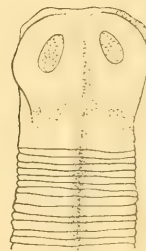
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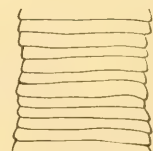
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## PLATE XII

## EXPLANATION OF PLATE

Fig. 133.—*Proteocephalus fossatus* (Riggenbach), head, toto. After Riggenbach.

Fig. 134a & b.—*Proteocephalus ambloplitis* (Leidy), head (a) and part of strobila (b). After Leidy.

Fig. 135.—*Proteocephalus exiguus* La Rue, entire worm. After Benedict.

Fig. 136.—*Proteocephalus exiguus* La Rue, entire worm. After Benedict. These two figures show the variation in length of neck.

Fig. 137.—*Proteocephalus exiguus* La Rue, head, frontal section. After Benedict. Shows structure of the functional fifth sucker.

Fig. 138.—*Proteocephalus exiguus* La Rue, head, toto showing fifth sucker. After Benedict.

Fig. 139.—*Ophiotaenia nattereri* (Parona), head, toto. After Schwarz.

Fig. 140.—*Ophiotaenia racemosa* (Rud.), head, toto. After Schwarz.

Fig. 141.—*Ophiotaenia trimeresuri* (Parona), head, toto. After Parona.

Fig. 142.—*Ophiotaenia trimeresuri* (Parona), head, toto. After Parona.

Fig. 143.—*Proteocephalus salvelini* (Linton), head, toto. After Linton.

Fig. 144.—*Proteocephalus salvelini* (Linton), head. After Linton.

Figs. 145, 146.—*Proteocephalus torulosus* (Batsch), heads, toto. After Batsch.

Figs. 147, 148.—*Proteocephalus dubius* La Rue, heads, toto. After Zschokke.

Fig. 149.—*Proteocephalus dubius* La Rue, proglottid. After Zschokke.

Fig. 150.—*Proteocephalus fallax* La Rue, head, toto showing fifth sucker. After Krämer.

Fig. 151.—*Choanoscolex abscisus* (Riggenbach), head, toto. After Riggenbach.

Fig. 152.—*Proteocephalus skorikowi* (von Linstow), head, toto. After von Linstow.





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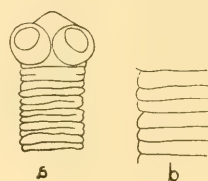
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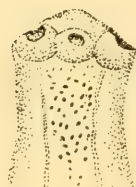
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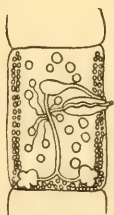
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## PLATE XIII

## EXPLANATION OF PLATE

Fig. 153.—*Ophiotaenia punica* (Cholodkovski), head, toto. After Cholodkovski.

Fig. 154.—*Monticellia malopteruri* (Fritsch), head, toto. After Fritsch.

Fig. 155.—*Ophiotaenia calmettei* (Barrois), head, toto. After Schwarz.

Fig. 156.—*Ophiotaenia calmettei* (Barrois), head, toto. After Marotel.

Fig. 157.—*Monticellia diesingii* (Monticelli), head, toto. After Monticelli.

Fig. 158.—*Proteocephalus agonis* (Barbieri), head, toto. After Barbieri.

Fig. 159.—*Proteocephalus cyclops* (v. Linstow), head, toto. After von Linstow.

Fig. 160.—*Ophiotaenia pigmentata* (von Linstow), head, toto. After von Linstow.

Fig. 161.—*Proteocephalus osculatus* (Goeze), head, toto. From Carus after Wagener. This appears to be a reproduction of Goeze's figure.

Fig. 162.—*Proteocephalus osculatus* (Goeze), young individual, toto. From Carus after Wagener.

Fig. 163.—*Proteocephalus osculatus* (Goeze)=*Taenia alternatim transverse lineata*, posterior proglottids, toto. After Goeze.

Fig. 164.—*Proteocephalus osculatus* (Goeze)=*Taenia alternatim transverse lineata*, head and regions of strobila. After Goeze.

Fig. 165.—*Proteocephalus osculatus* (Goeze)=*Taenia alternatim transvers lineata*, head, toto. After Goeze.





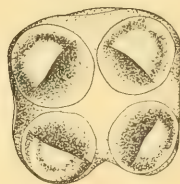
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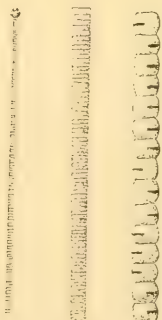
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## PLATE XIV

## EXPLANATION OF PLATE

Fig. 166.—*Proteocephalus malopteruri* (Fritsch), ripe proglottid. Modified from Fritsch's figure.

Fig. 167.—*Proteocephalus longicollis* (Zeder), ripe proglottid. Modified from drawing by von Linstow.

Fig. 168.—*Proteocephalus longicollis* (Zeder), ripe proglottid, cross-section. After von Linstow. Note that the testes lie in more than one layer.

Fig. 169.—*Proteocephalus longicollis* (Zeder), cirrus-pouch. After von Linstow.

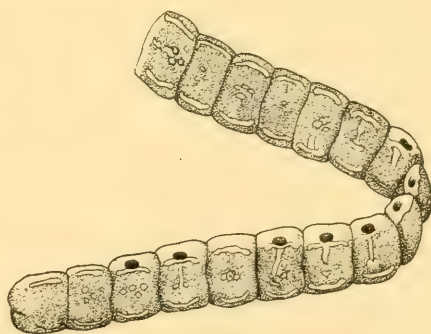
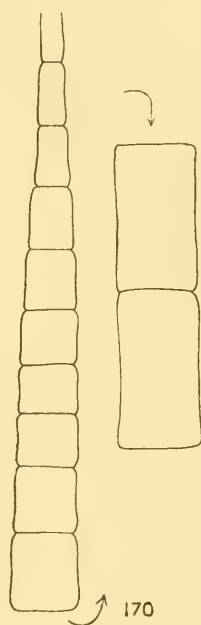
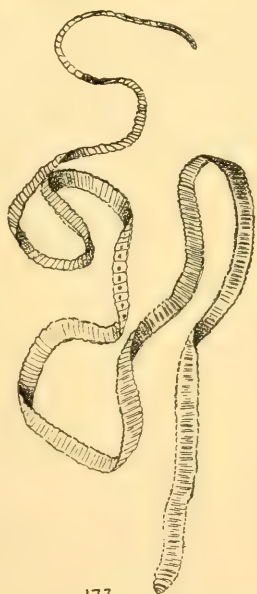
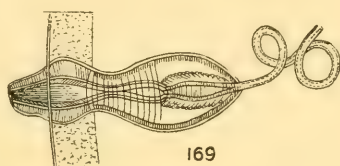
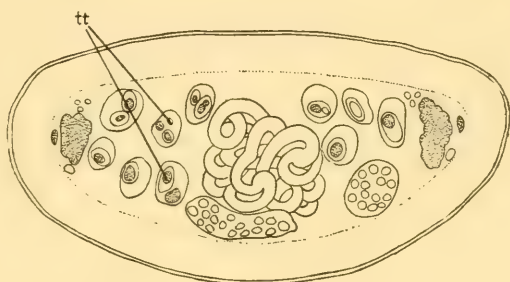
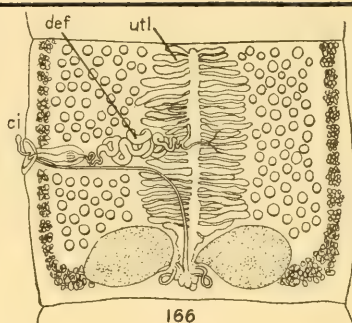
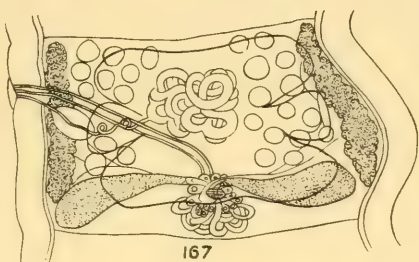
Fig. 170.—*Proteocephalus fallax* La Rue, outline of proglottids from anterior and posterior parts of strobila. After Krämer.

Fig. 171.—*Proteocephalus macrocephalus* (Creplin)=*Taenia dilatata* Linton, folds of tissue along neck. After Linton.

Fig. 172.—*Proteocephalus percae* (Müller), piece of strobila. Reproduction of Müller's figure 4.

Fig. 173.—*Proteocephalus percae* (Müller), strobila. Reproduction of Müller's figure 1.







## PLATE XV

## EXPLANATION OF PLATE

Fig. 174.—*Proteocephalus agonis* (Barbieri), ripe proglottid. After Barbieri.

Fig. 175.—*Proteocephalus sulcatus* (Klaptocz), ripe proglottid. After Klaptocz.

Fig. 176.—*Proteocephalus sulcatus* (Klaptocz), proglottids. After Klaptocz.

Fig. 177.—*Proteocephalus skorikowi* (von Linstow), ripe proglottid, toto. After von Linstow.

Fig. 178.—*Proteocephalus fallax* La Rue, mature proglottid, toto, showing reproductive organs. After Krämer.

Fig. 179.—*Proteocephalus fallax* La Rue, ripe proglottid, showing uterine pouches and uterine pore. After Krämer.

Fig. 180.—*Proteocephalus fossatus* (Riggenbach), proglottid with male organs. After Riggenbach.

Fig. 181.—*Monticellia coryphicephala* (Monticelli), cirrus-pouch and vagina. After Monticelli.

Fig. 182.—*Proteocephalus osculatus* (Goeze), mature proglottid. After Lühe.

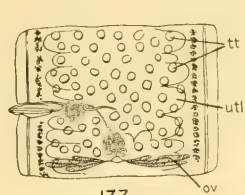
Fig. 183.—*Proteocephalus ambloplitis* (Leidy), ripe proglottid, frontal section showing main parts of male and female reproductive systems. After Benedict.

Fig. 184.—*Proteocephalus torulosus* (Batsch), ripe proglottids showing organs. After Krämer.

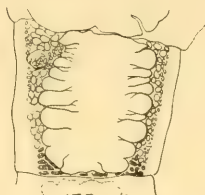
Fig. 185.—*Proteocephalus agonis* (Barbieri), mature proglottid, uterus omitted. After Barbieri.

Fig. 186.—*Monticellia coryphicephala* (Monticelli), ripe proglottid, toto. After Monticelli.

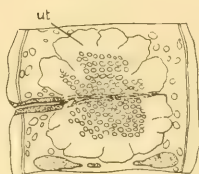




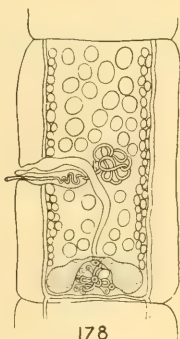
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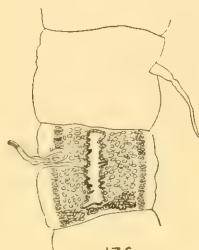
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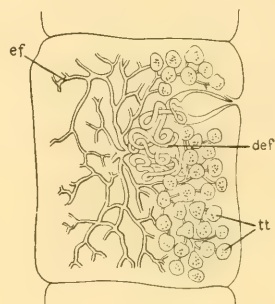
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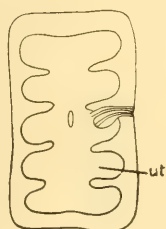
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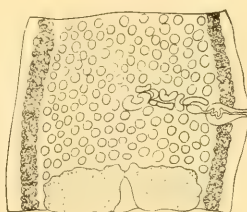
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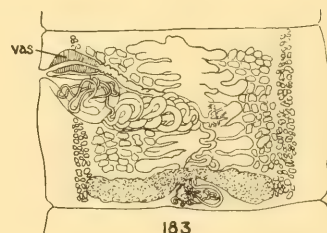
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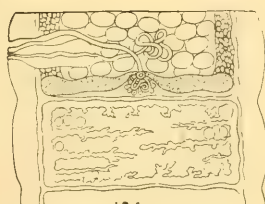
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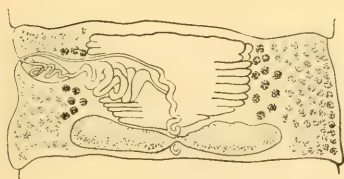
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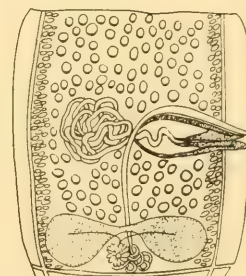
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## PLATE XVI

## EXPLANATION OF PLATE

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Fig. 188.—*Ophiotaenia punica* (Cholodkovski), young proglottids, toto. After Cholodkovski.

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Fig. 199.—*Ophiotaenia marenzelleri* (Barrois), mature proglottid, toto. After Schwarz.



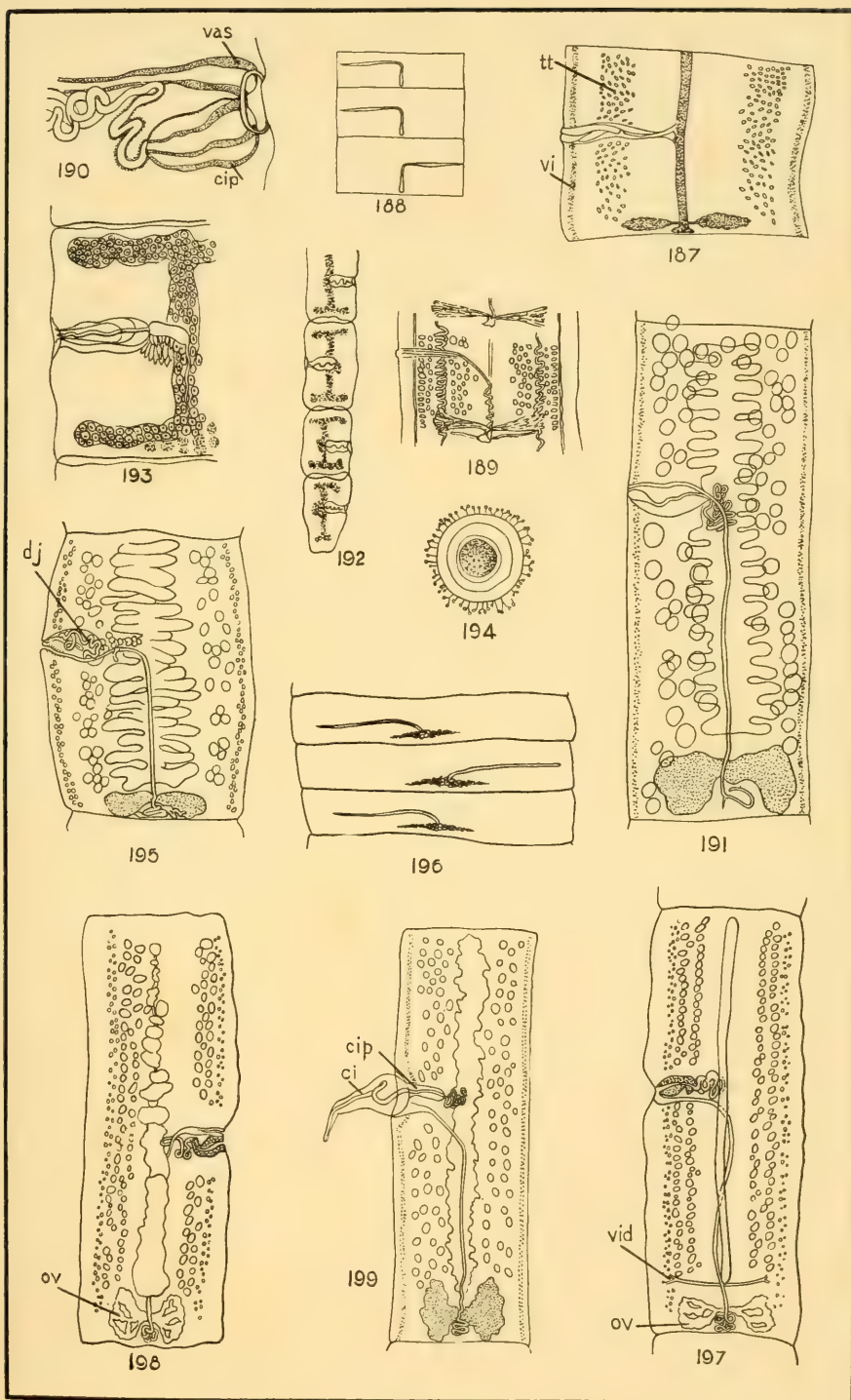


PLATE XVI



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EDITORIAL COMMITTEE

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STUDIES ON  
THE CESTODE FAMILY  
ANOPLOCEPHALIDÆ

WITH SIX PLATES

BY

HERMAN DOUTHITT

Contributions from the  
Zoological Laboratory of the University of Illinois under the direction of  
Henry B. Ward, No. 38

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## INTRODUCTION

The present paper gives the results of studies begun at the University of Illinois in December, 1910, and carried on, between numerous interruptions, to the present time.

My purpose has been to make a comparative anatomical study of the Anoplocephalidae, but since so few of the individual representatives of the family have received adequate study, it has been necessary for me to give most of the time to the individual study of undescribed or poorly described species. The work lacks much of being complete; many of the genera I have not had opportunity to study myself. Other work compelled me to lay the task aside, and it seems advisable to make public the results already obtained.

My thanks are due to Professor Henry B. Ward for assistance of many sorts; to Professors Robert T. Young, M. J. Elrod, and R. A. Lyman, Drs. B. H. Ransom, and John E. Gutberlet, for materials placed at my disposal for study; also to Miss Bertha E. Martin for criticisms and assistance in preparing manuscript.

## ANATOMICAL DESCRIPTION OF SPECIES AND GENERA

### *Andrya primordialis* sp. nov.

[Figures 1-4]

Two specimens of this cestode, one without scolex, were taken from a red squirrel (*Sciurus hudsonica*) at Bemidji, Minnesota, in September, 1911. Since about 20 squirrels in all were examined, there and at Brainerd, Minnesota, it seems that this species is rare, at least as far as this region and host are concerned. Other species of squirrels from these and other localities were likewise uninfected with this species. Its close relationship to the ancestral types of the Anoplocephalidae seems evident, even tho based upon a study of so few specimens.

The worms, neither of which are fully grown, have a length of 40 mm. and the single complete specimen has 155 proglottids. The strobila increases in width to the posterior end, there being 1 mm. in breadth. The first proglottids are 290 $\mu$  wide and one-eighth as long. Mature proglottids are half as long as wide, and the proglottids farther back

are somewhat longer. The scolex is compact,  $700\mu$  long by  $475\mu$  broad, the greatest width being near the anterior end. Posteriorly the scolex tapers uniformly, until it merges into the neck, which is  $290\mu$  broad. The suckers open nearly directly forwards. A circular groove about the scolex at the level of the suckers makes it appear as if the tip of the scolex were contracted somewhat within the rest.

The genital pore is always on the right margin, about four-fifths the length of the proglottid from its anterior end. It is relatively large and deep as compared with the same organ in related cestodes. The cirrus pouch is much larger than in other known members of the genus, both in length and breadth, its median end lying well across the excretory ducts. Its inner end is rounded and its lateral end only slightly tapering. Across the middle its diameter is considerably less than at either end so that its outline is somewhat like that of the figure 8. The median end is occupied by the vesicula seminalis. The vas deferens is not enlarged nor greatly coiled. An elongated prostate gland lying in the anterior end of the proglottid empties into the vas deferens near the cirrus pouch. The testes are dorsal, occupying the entire median field to the left of and anterior to the vitelline gland and receptaculum seminis, and partly underlying the latter. In the distal half of the left side the testicular field extends laterad beyond the ventral excretory duct. The testes number 30 to 40 and are mostly 70 to  $80\mu$  long, the breadth being somewhat less. They break down early, but the membranes remain intact and the individual testes are easily distinguishable.

The vagina lies entirely posterior to the cirrus pouch, and in the same dorsoventral plane. Its coils are thickly beset with glandular cells. The receptaculum seminis is large and slightly longer anteroposteriorly than laterally. It lies directly in front of the vitelline gland, and does not reach laterad to the ventral excretory duct as is the case in other species of the genus. The ovary is a semicircular mass, reaching nearly across the median field. In immature stages 12 to 15 lobes can be distinguished which radiate in all horizontal directions; but before the ovary matures these lobes become indistinguishable. The ovary is not located nearer the pore side than the other, the mouth of the oviduct being as often to the left as to the right of the median line. The vitelline gland however is distinctly nearer the pore side. It is of the shape most usually found in this group, being composed of a large median and a smaller lateral portion connected by a transverse portion.

The uterus, just before sexual maturity, is a network of tubes in the anterior two-thirds of the proglottid. In the median field it extends distad to below the upper limit of the ovary, ventrad of the latter. The



lateral tips extend a little farther distad than the median portion and cross the excretory ducts ventrally on either side. The anterior and lateral margins together form a semicircle, so that at this stage the uterus as a whole is somewhat semilunar in outline. The early development of the uterus will be taken up later (page 51). Development from the stage just described is first by enlargement and coalescence of tubes, forming a saccular structure; then by regular outpocketing, anteriorly, distally, and laterally. The anterior and lateral pockets together number about 22; the distal, 15. Since neither specimen possessed completely ripe proglottids, a study of the embryo was unfortunately not possible.

The dorsal excretory duct lies laterad of the ventral and usually somewhat more dorsal. The diameter of the ventral is  $30\mu$  and that of the dorsal  $7\mu$ . The transverse commissure is of very small diameter and is not visible at all in sections at hand except in proglottids past sexual maturity.

The presence of the prostate gland and the reticulate uterus show at once that this species is allied to the genus *Andrya*. It disagrees however with the accepted diagnosis in that (1) the pores are strictly dextral, (2) the ovary is not nearer the pore side than the opposite side, (3) the testes extend laterad across the ventral excretory duct on the aporose side; and (4) the later development of the uterus is by regular anterior and posterior outpocketing.

The first point of disagreement is not an important one since unilaterality is approached in all of the species of the genus. The second point, while significant in other aspects cannot be regarded as of generic import since the other female glands are displaced in the regular manner. The third point will be shown to be true also of known and new species of *Andrya*, *Anoplocephala*, and *Bertiella*; so that the descriptions of these genera are in error, and this character, supposed to be confined to the genus *Aporina*, is found in all the single-pored genera of the subfamily except *Schizotaenia*. As to the fourth, the discrepancy seems to be due to errors in the descriptions of the species already known; for while Stiles (1896), describing the uterus of *Andrya rhopalocephala* says it is in its final stages a simple sac or with "at most extremely fragmentary and rudimentary divisions", his figures of gravid uteri of this species and *A. cuniculi* (see his Plate VIII, fig. 1 and Plate IX, fig. 1) show for both species what is apparently regular outpocketing, correctly drawn tho misinterpreted.

This cestode shows several characters which mark it as the most primitive species known in the genus; and if the contention later made

be accepted, that *Andrya* is the most primitive genus of the family, then this becomes the most primitive known species. Its primitive characters are (1) the very broad distribution of the testes which occupy nearly the entire median field and part of the lateral; (2) the fact that the ovary is not nearer the pore side than the opposite side; and (3) the limitation of the receptaculum seminis to the median field and its simple globular character. In these characters this species is approached in some respects by *A. communis*, next to be described, which must be regarded as its nearest known ally.

*Andrya communis* sp. nov.

[Figures 5-8]

Professor R. T. Young collected in 1908 at Long's Peak, Colorado, cestodes from *Evotomys gapperi galei*, *Microtus pennsylvanicus modestus* and *Peromyscus* sp. They were examined by Hall who concluded and reported (1912) that those from *Evotomys* and *Microtus* represented a species of *Anoplocephala*, while those from *Peromyscus* represented a second species of the same genus. Professor Ward has secured for me the loan of this material for study. The cestodes from *Peromyscus* belong really in the genus *Hymenolepis*, except for one slide, apparently mislabelled, which is of the same species as those from *Microtus*. Those from *Evotomys* and *Microtus* prove to be two distinct species, the first being an *Andrya* and the other probably an *Andrya* also, tho the fragments at hand are all too far past sexual maturity to allow of certain generic determination. The latter species must therefore of necessity be omitted from consideration, tho it comes within the scope of this paper.

The species under consideration from *Evotomys gapperi galei* is represented in the material at hand by about 200 fragments in alcohol and 17 slides, most of which were prepared by Professor Young. Only one scolex is in this lot, this being in the form of oblique cross sections. Recently I have found in the collection of Professor Ward four fragments, evidently representing one worm, which were of the same lot of material, and were presented to Professor Ward several years ago by Professor Young. This material includes a scolex with a considerable number of proglottids attached, thus furnishing an idea of the appearance of the complete worm.

The total length is estimated to be about 3 or 4 cm; the number of proglottids, about 225. The greatest width is about 1.5 to 2 mm. The proglottids vary in shape from 12 times as long as broad shortly before

sexual maturity to longer than broad in the case of ripe proglottids. The length of the scolex is roughly  $560\mu$ . The greatest width,  $350\mu$ , is reached  $95\mu$  from the anterior end. The anterior end is rounded; posteriorly the scolex narrows regularly.

The genital pores are all on the right margin near the middle of the proglottid. The circular muscles surrounding the inner end of the cirrus pouch are usually contracted, compressing this part and making the pouch inversely pear-shaped. In older proglottids however the inner end becomes distended and much larger than the outer. In some specimens the cirrus pouch is separated by a distance equal to its own length from the ventral excretory duct; in others its median end extends across both ducts (Figs. 5 and 8). The different conditions do not seem to depend so much on the stage of contraction of the proglottid as upon differences in the position of the excretory ducts. An internal vesicula seminalis is present. The cirrus is generally extruded, tho usually it does not extend outside the genital pore.

The vas deferens is not enlarged and is not coiled, tho it is probable that some coiling would be found in more expanded specimens. A distinct prostate gland is present; it is tubular with a globular enlargement at its end. Lateral to the pore of the prostate gland the vas deferens is surrounded by a loose cellular mesh. The testes are all dorsal. On the left they may extend across both excretory ducts, or they may be strictly limited to the median field. To the right they extend as far as the prostate gland in the anterior part of the field. They extend distad as far as the vitelline gland and receptaculum seminis, and on the left of these they extend to the distal end of the proglottid. The number varies in eight proglottids counted from 24 to 41. They are mostly transversely elongated,  $55$  to  $80\mu$  long in transverse axis by  $30$  to  $50\mu$  in longitudinal axis.

The vagina lies entirely posterior to the cirrus pouch and vas deferens and in the same plane. Up to the beginning of the receptaculum seminis its walls are glandular. The receptaculum begins where the vagina crosses the dorsal excretory duct; it enlarges gradually and uniformly to near its inner end then becomes abruptly smaller. The ovary is an asymmetrical mass most of whose bulk lies on the pore side, but it approaches no nearer to the excretory ducts on one side than on the other and the oöcapt is as often to the left as to the right of the median line. It shows rather obscure and uncertain evidence of partial division into about seven radiating lobes. The lateral and median lobes of the vitelline gland are but little larger than the transverse portion of the gland which connects them. This gland lies considerably to the pore side of the median line.



The uterus is a typical reticulum in its early stages. It lies entirely anterior to and to the left of the ovary, being never ventrad of it. To the left of the ovary it reaches the transverse commissure posteriorly. On either side it crosses the ventral excretory ducts ventrally. Development from this stage is as in *A. primordialis*.

The excretory ducts are dorsal and ventral in position in the head region; but the dorsal duct very early moves to a position laterad of the ventral, which it retains. The ventral duct is four times the diameter of the dorsal; the transverse commissure is very small. The ventral duct diverges from the central axis as it passes distad until near the distal end of the proglottid where it turns almost directly mediad to regain its position. The dorsal duct has a somewhat similar course but not so pronounced.

This cestode it will be seen is rather closely related to *Andrya primordialis*. Many of the differences in the two accounts are due probably to differences in the state of contraction in the material.

*Andrya macrocephala* sp. nov.

[Figures 9-13]

Fifteen specimens of this species were taken from pocket gophers (*Geomys bursarius*) living in swampy river bottom land at Brainerd, Minnesota, and one from a gopher living in low, heavy, black soil at Thief River Falls, Minnesota. Apparently they are entirely absent from sandhill regions if not from all uplands. For distribution and frequency see the table on page 62.

By far the most conspicuous anatomical feature of this cestode is the enormous development of the ventral excretory ducts and commissures. In the scolex anterior to the distal end of the suckers, the four ducts have a winding course, the diameter of each varying generally between 18 and 32 $\mu$ . Distad of the suckers the ducts have a straight course, are approximately 15 $\mu$  in diameter, and are arranged as a dorsal and a ventral pair. Near the distal end of the scolex the dorsal duct begins to move laterad and soon comes to lie directly laterad of the ventral. The diameter of the dorsal duct throughout the strobila is about 18 $\mu$ . The ventral ducts increase considerably in size as they pass distad. As the proglottids approach sexual maturity this increase becomes much more rapid and the transverse commissures appear and develop rapidly. In a sexually mature proglottid the ventral aporose duct near the middle of the proglottid is 80 $\mu$  in transverse diameter; at either end it is 145 $\mu$  in diameter. On the pore side the transverse diameter is 125 $\mu$  in the center; at either end, 150 $\mu$  or more. The



dorsoventral diameter in the center is  $225\mu$ . The transverse commissure measures at its largest point about  $100\mu$ ; at either end it becomes smaller. As the proglottids age the ducts keep on increasing in size. The largest dimensions observed for the transverse commissure were  $320\mu$ ; for longitudinal ducts, exclusive of interproglottidal enlargements, both transverse and dorsoventral diameters reached  $320\mu$ ; for interproglottidal enlargements,  $430\mu$ . As the proglottids lengthen prior to detachment, the ducts become smaller as the result of the stretching, and the interproglottidal enlargements which are not thus affected become prominent as spindle-shaped objects.

Since the maximum breadth of this worm is 1.5 mm. it will be seen that this development is truly enormous, the two ventral ducts extending in some cases through not far from one half the transverse measurement of the proglottid and dorsoventrally through the cortical layer. This is not due to reagents since the living worms exhibit the enormous ducts clearly visible to the naked eye, before being given any treatment whatever. Great as this development is however it will be seen that it is exceeded in *Andrya translucida*, the next form to be considered, tho with the difference that in the present species the dimensions are constant in any given stage of development of the proglottid while in the other they will suddenly develop enormously and then as suddenly decline. These enormous ducts make these two species quite transparent in life.

The cestode is contractile when alive; it is from 10 to 20 cm. long and is composed of from 345 to 455 proglottids, the average of 14 specimens being 393. In well expanded specimens the neck is 1.5 mm. long, in one case even 3 mm. while in some contracted specimens it is only 0.3 mm. The diameter varies from 0.2 to 0.6 mm. The strobila increases in width gradually to reach the maximum width of 1.5 mm. about one-third of its length from the anterior end. From this point back the width remains about constant. Sexually mature proglottids, which begin about the 145th in the strobila, measure in a typical specimen 0.3 mm. long by 0.9 mm. broad.

The very large scolex is nearly globular in form, being 600 to  $800\mu$  wide and 700 to  $950\mu$  long; eleven specimens which were measured averaged  $709\mu$  wide by  $811\mu$  long. One finds but slight indications of grooves between the suckers; the very shallow depressions fade out before reaching the apex. The suckers are very large, thin-walled structures, usually collapsed and opening directly forwards. Their diameter is  $300\mu$  and their depth,  $415\mu$ . Their muscular wall is  $50\mu$  thick and the orifice is  $50\mu$  across.

The genital pore is on the right margin, two-thirds the length of the proglottid from the anterior end. The cirrus pouch is a stout, pearshaped structure,  $155\mu$  long,  $75\mu$  in diameter at its inner end, and  $35\mu$  in diameter at its outer. The tip of the pouch lies dorsad of the ventral excretory canal just within its lateral boundary. Part of the vesicula seminalis lies within the pouch; a much larger portion lies without, dorsad of the ventral excretory duct and extending mediad of it. There is no prostate gland. The testes are dorsal, extending nearly if not entirely across the median field, and into the lateral field on the side away from the genital pore. On the pore side of the field they are confined to the region anterior to the ovary; on the opposite side they are slightly more posterior than anterior. They number 43 to 57 in eight proglottids counted and average about  $50\mu$  long, being slightly smaller in other dimensions. They break down early but each remains distinct within its membrane.

The vagina lies entirely posterior to the cirrus pouch, and in the same dorsoventral plane. Its walls are beset with glands. Dorsad of the ventral excretory duct and extending beyond it on either side is the very large receptaculum seminis which is somewhat constricted in the middle, giving it a two-lobed appearance. The ovary consists of about 15 distinct lobes, which radiate in all directions from the point of origin of the oviduct. The posterior lobes, which are much shorter than the rest, extend distad on the ventral side of the transverse commissure to near its posterior limit. The oviduct begins just anterior to the transverse commissure, four-tenths of the diameter of the proglottid from the pore margin.

The uterus is reticular tho there is a tendency for the tubes not to develop. The uterus thus tends to become what might be termed diffuse. Certain main ducts develop regularly; the rest of the cavity is usually formed by the mere expansion of these. In front of the ovary, near the median line, the uterus is represented by a single tube; to the right and left it widens distally until near the excretory ducts; it then crosses beyond these ventrally. The later development of the uterus is by regular outpocketing. The embryo is about  $20\mu$  in diameter. It bears a large pyriform body whose length plus that of the embryo is  $30\mu$ . The outer embryonic membranes are mostly elongate; when spherical, the outer membrane has a diameter of 30 to  $32\mu$ . The middle membrane is loose fitting and irregular. The uterus of this species is almost identical with that of the genus *Andrya* and therefore different from that of other closely allied genera. Likewise the distribution of the testes is fundamentally the same. This species however disagrees with other known *Andryae* in that it has no prostate gland, and in that

it has a well developed external vesicula seminalis. The extraordinary development of the ventral excretory system, moreover, is a character of which one finds no suggestion in its nearest allies. These points argue strongly for generic distinctness for this and the next species. Whether to create for them a distinct genus or include them in the genus *Andrya* is a question. However the uterine structure and testicular distribution, combined with certain other undefinable resemblances seem evidences of sufficiently close generic kinship to the known species of *Andrya* to permit the inclusion of these forms in this genus. Yet the diagnosis of the genus *Andrya* must be altered so as to admit these species.

*Andrya translucida* sp. nov.

[Figures 14-16]

Three specimens of this cestode were taken from a pocket gopher (*Geomys bursarius*) from low, semi-swampy river bottom land at Brainerd, Minnesota. The same gopher yielded also five specimens of *A. macrocephala* to which it is evidently closely related. Since a great many gophers were examined in this and other localities (see table, page 62) it would seem that the species is a rare parasite of the gopher.

The total length of the specimens at hand is 9 to 12 cm. The number of proglottids is 278 to 289. The greatest diameter of the strobila, 0.75 mm., is reached 3 cm. from the anterior end. Back of this the proglottids become longer and narrower, the most posterior becoming attenuated and some of those at hand measuring 0.3 mm. wide by 1.3 mm. long. The worm is quite transparent in life, due to the enormous development of the excretory ducts.

The scolex is 730 to 830 $\mu$  long by 590 to 640 $\mu$  wide. The suckers stand out rather prominently and are separated from each other by distinct grooves. They open obliquely forward, through orifices about 110 $\mu$  across. A definite neck is present, 500 to 730 $\mu$  in length and 350 to 410 $\mu$  in diameter.

The genital pore is usually on the right margin but frequently a number of adjacent proglottids have their pores on the opposite side. The pore is located seven-tenths of the length of the lateral margin from the anterior end of the proglottid. The cirrus pouch at the time the sperms begin to enter is usually short and thick, being 75 $\mu$  long by 40 $\mu$  broad, and lying wholly laterad of the ventral excretory duct. In succeeding proglottids it lengthens rapidly, becoming 160 $\mu$  long by 40 $\mu$  wide at its inner end which lies mediad of the ventral excretory duct. The vesicula seminalis occurs both within and without the pouch, being represented without by a coiled tube which is about five times the



diameter of the vas deferens and extends forward and mediad in front of the receptaculum. The testes are usually confined entirely to the side opposite the pore but two or three may lie on the pore side of the median line; however they do not reach as far as the median line of the vitelline gland. Likewise, the testes are nearly all in the distal half of the proglottid. In both these features is seen a superficial resemblance to *Anoplocephala*. The testes extend well across the ventral excretory duct laterally. When not disturbed by the ventral excretory duct they extend entirely thru the medullary portion.

The vagina lies ventral of the cirrus pouch. Laterad of the excretory ducts its walls are glandular. Very early, long before sexual maturity, it expands at its inner end forming a receptaculum seminis. This cavity grows and extends laterad until it reaches the outer edge of the dorsal excretory duct. It is largest at its inner end and its diameter decreases gradually laterad so that it merges imperceptibly into the unenlarged portion of the vagina. The ovary is formed of about 15 lobes which radiate anteriorly, distally, and laterally; the female glands are situated slightly to the pore side of the median line. The vitelline gland is of rather unusual shape, owing to the size of the median lobe and its encroachment on the space within the circle of the gland.

The uterus is a very simple reticulum with its different branches wide apart and clearly distinct from each other. It lies anterior to the ovary and extends laterad to beyond the excretory ducts on either side. In front of the ovary two or three transverse tubes are to be found; in the lateral regions, six or eight. The lateral development of the proglottids is very peculiar, and apparently abnormal, in that the ova do not pass into the uterus. In one specimen, having in all 278 proglottids, the uterus had already begun to develop in the earliest proglottid sectioned, number 148. In proglottid number 186 the receptaculum had reached its full development and was filled with sperms. In succeeding proglottids it was fully developed but nearly always empty. Proglottid number 187 showed all evidences of sexual maturity. The vesicula and receptaculum are developed, and the branches of the netlike uterus have become open tubes. In the following 91 proglottids however only 11 uteri contain eggs, these being between the 222d and 240th proglottids. The uterus is distinguishable in all except the most posterior, attenuated proglottids; it never develops beyond the reticular stage. In proglottid number 260 the degeneration of the ovary is nearly complete. The other two cestodes at hand of this species were cleared and examined in toto. They showed the same condition; in only an



occasional uterus are eggs present. These two individuals have each 289 proglottids; in all three cases some proglottids have been shed.

I can offer no certain explanation of this condition. The genital ducts appear normal and the ova certainly do not pass into any other organ than the uterus. There can hardly be any doubt therefore that these cestodes were incapable of perpetuating themselves. To find the end proglottid, or even several of the terminal proglottids sterile would not be surprising; but to find nearly a hundred such in individuals that have already shed some of their proglottids is certainly not to be expected. Such a condition could of course arise as a mutant, incapable of perpetuating itself; in this case it could hardly be thought to have arisen from *Andrya macrocephala*, the nearest known relative; for while these and that species resemble each other in a general way, they differ in nearly every organ. A more probable explanation seems to be that the gopher is not the normal host and that sterility has resulted from unnatural conditions of environment. Sterility as a result of unnatural environment is a very common phenomenon in both animals and plants; and there is no reason why the condition might not be found in cestodes. Each of these explanations is favored by the fact that the three individuals were all found in the same host and were of the same size and appearance, making it appear probable that they arose from a single infection.

The excretory ducts show striking features also. As in *A. macrocephala* the ventral ducts are enormously developed. In this case the development is much greater however, especially that of the transverse commissure, so that often the proglottid is nearly separated by the excretory ducts into dorsal and ventral parts, the testes being dorsal and the ovary and uterus ventral. The transverse commissures are frequently three or four times as wide as the space between them; and when the ventral longitudinal ducts are likewise thus developed, the medullary space within these commissures becomes a mere patch in the anterior part, not much larger than is necessary to contain the vitelline glands and the female ducts. This enormous development is not constant however; such a development as described may be in a proglottid adjacent to one with ventral ducts  $60\mu$  in diameter. This is still an unusual size but is not greater than that found regularly in *A. macrocephala*. The dorsal duct has a rather sinuous course and is of ordinary size. It lies laterad of the ventral.

Altho differing in practically every organ from *A. macrocephala*, there is a fundamental resemblance between these two which argues for generic relationship. The similarity to Anoplocephala in the distribution of testes is interesting but is not to be taken as of more than specific

import, since such a condition is easily derived from *Andrya* by the suppression of the most anterior testes.

#### ANATOMICAL CHARACTERISTICS OF THE GENUS ANDRYA

The additions here made to the knowledge of the genus *Andrya* necessitate a radical revision of our conception of the group. These changes, briefly, are as follows:

1. The definition must be changed so as to admit forms in which the testes cross beyond the excretory ducts on the side away from the genital pore. Also, the fact that *A. translucida* has the testes only on the side away from the pore and mainly in the distal part of the proglottid, must be recognized. In the way of more exact definition it should be stated that the testes are always chiefly found on the side away from the pore and usually mainly anterior.

2. The strictly dextral arrangement of the genital pores which is found in some species, must be given recognition.

3. It must be recognized that the ovary may be directly median in position.

4. It must be recognized that the later development of the uterus is by outpocketing, in a manner not different from that occurring in *Anoplocephala* and *Bertiella*.

5. The definition must be changed so as to admit species without a prostate gland.

6. The position of the vagina and vaginal pore has been shown to be a constant character and should be given recognition.

7. The point of origin of the oviduct should be mentioned as a distinction from *Schizotaenia*.

The diagnosis of *Andrya* then becomes as follows:

Anoplocephalinae, with segments much broader than long, except in the most distal parts of the strobila. A single set of reproductive organs to each segment. Genital pores mostly, or entirely dextral. Genital canals pass dorsal of longitudinal excretory vessels and nerves. Testes chiefly on the side away from the genital pore, usually mainly anterior, and usually extending nearly across the median field anteriorly; on the side away from the pore they usually extend beyond the excretory ducts. Vagina and vaginal pore strictly posterior to the cirrus pouch. Female glands on the pore side of the median line, or with the ovary median. Oviduct connects with ovary beneath the median lobe of the vitelline gland. Uterus reticular, becoming saccular,

then developing by regular anterior and posterior outpocketing. Eggs with pyriform apparatus. Adults in mammals.

Type-species: *Andrya rhopalocephala* Riehm 1881.

Representing the genus *Andrya*, six species are known; besides those here studied, these are *rhopalocephala* and *cuniculi* (for both of which see Stiles, 1896). In addition, Parona (1900) has designated a cestode from *Dypus aegyptius* as *A. dipi*, with no word of description. As it is a pure nomen nudum, it can not be taken into consideration. The six known species fall into two well-defined groups, the rank of which it is difficult to decide. They are here treated as subgenera:

1. *Rhopalocephala*-group. Testes mainly anterior. With a pedunculated prostate gland opening into the vas deferens near the ventral excretory vessel. Vas deferens not enlarged outside the cirrus pouch to form a vesicula seminalis. Excretory ducts of normal dimensions. Scolex normal in size. Four species.

*A. rhopalocephala* Riehm      *A. primordialis* Douthitt

*A. cuniculi* R. Blanchard      *A. communis* Douthitt

2. *Macrocephala*-group. Testes about uniformly anterior and posterior, or mostly posterior. No prostate gland. Vas deferens enlarged to form a vesicula seminalis outside the cirrus pouch. Excretory ducts enormously developed. Scolex of more than ordinary size. Two species:

*A. macrocephala* Douthitt      *A. translucida* Douthitt

*Anoplocephala wimerosa* Moniez 1880

[Figure 17]

Of this species but two specimens are at hand. Admittedly, this is not sufficient material to form a basis for a satisfactory account of anatomy; but there is need to know the structure of the older members of this genus, for comparison with the better known new ones, which do not fit old conceptions. *A. wimerosa* has been known for 33 years; but it has received scanty attention, and several of the statements concerning it I find to be in error.

The specimens studied were taken from *Lepus variabilis* at Briançon, France, by R. Blanchard in 1891. He gave several specimens to Stiles, who, after he had studied them, divided the lot, presenting two to the Ward Collection. These were placed at my disposal for study. One is a toto mount and the other was sectioned. The account here given is original, except for the statements applying to external form which are taken from the account of Stiles (1896).



*Anoplocephala wimerosa* has a length of 10 mm. and a breadth of 1.5 to 2.25 mm., and contains 10 to 28 proglottids. The proglottids are much broader than long, except the distal segments, which rarely become as long as broad. The head is 0.7 to 0.88 mm. in diameter, is cuboid in form, and is quite distinct from the strobila. The suckers are 0.4 mm. in diameter, are prominent, and open diagonally forward.

As would be expected in so short a strobila, each proglottid shows a distinct advance in development over the one before. The genital organs are fairly well formed in the first proglottid. The receptaculum seminis begins to fill with spermatozoa in the fifth. By the fifteenth the testes have practically disappeared, and the receptaculum, vesicula, and cirrus pouch are enormously distended with spermatozoa. A few remnants of the testes persist until the eighteenth. The ovary develops to its full size in the eighth or ninth proglottid and begins to discharge eggs into the uterus. In the next proglottid this process is completed and the ovary disappears.

The testes, which are frequently as much as  $90\mu$  long, are irregular in shape. They occur on the side away from the pore and reach laterad to beyond the excretory ducts. The number, in six proglottids counted, ranged from 31 to 42. Not more than two testes can lie in a row in the axis of the strobila. The cirrus pouch is enormous. In a mature proglottid it is  $520\mu$  long and at its inner end extends thru the entire length of the proglottid. Its median end is occupied by a portion of the vesicula seminalis,  $190\mu$  long. The portion of the vesicula outside the pouch has a length in mature proglottids of  $100\mu$  and is two-thirds as wide. In older proglottids the entire vesicula becomes much larger. The cirrus pouch lies of necessity almost entirely mediad of the excretory ducts.

The genital pores are dextral. When undisturbed, the cloaca is  $200\mu$  deep. When the proglottid enters the period of sexual activity, it turns inside out. In the third or fourth segment succeeding, it is again drawn back. In this feature and in the enormous size of the cloaca and the cirrus pouch this cestode recalls *Schizotaenia*, especially *S. anoplocephaloides*, described in this paper. The unexpanded portion of the vagina is about  $300\mu$  long. Throughout its entire length it lies ventrad of the cirrus pouch, as does also the vaginal pore. No indication of glandular structure in its walls was observed. The receptaculum seminis is  $300\mu$  long in mature proglottids and at its median end extends from the anterior to the posterior border of the proglottid. Latterly it narrows regularly and evenly. In succeeding segments it becomes enormously distended.



The toto mount shows the whole of the female glands to be situated slightly to the pore side of the median line; the other specimen shows decidedly the opposite conditions in most proglottids. The shell gland is very indistinct in the material at hand. Nothing could be made out concerning its structure. The vitelline gland is  $135\mu$  long in transverse measurement. The posterior border is straight. Near the left end the gland measures  $76\mu$  across anteroposteriorly; it narrows somewhat towards the right until  $40\mu$  from the end; it then narrows abruptly. The ovary in immature proglottids consists of ten lobes which radiate anteriorly and laterally from a transverse portion. In its fully developed stage, however, no such divisions can be recognized. The ovary has a width of  $420\mu$  and extends practically through the proglottid anteroposteriorly. It reaches its full development in the eighth or ninth proglottid and disappears completely in the succeeding one.

The uterus begins as a simple transverse tube which seems to be confined wholly to the region between the excretory ducts. It develops mostly by expansion of the primary lumen, this occurring first at the end away from the genital pore. Short anterior and posterior outpocketings are present. In toto mount it appears as if these pockets are separated by a considerable space from each other; this is due to the fact that the eggs are shrunken, the outlines of the egg-masses being taken for the outlines of the pockets. As the uterus becomes filled with eggs it appears to force itself into the region ventrad of the excretory ducts. The embryos in the uterus have three shells. The outer is usually somewhat compressed; when spherical it measures  $48\mu$  to  $55\mu$  in diameter. The embryo itself measures  $13\mu$  to  $15.5\mu$  in diameter. The length of the embryo plus the pyriform body is  $17.5\mu$  to  $21\mu$ . The appearance of the horns of the pyriform body could not be made out. These measurements would probably not hold true for fresher material. It was not possible to make out much concerning the excretory ducts. The dorsal duct lies laterad of the ventral, and usually, at least, in the same plane. The two ducts appear to be approximately equal in size. Transverse commissures are present, but can be made out only with difficulty.

It will be seen that this species is without doubt an *Anoplocephala*. Yet it disagrees with the accepted conception of the genus in that the testes are not confined to the median field, and in that the female glands may not be placed to the pore side of the median line. Both of these conditions were found in *Andrya*, where they were supposed not to occur; and the first was found also in another species of *Anoplocephala*; they cannot therefore be regarded as generic differences. The diagnosis

of the genus *Anoplocephala* must of course be altered to conform; this matter is taken up later on.

*Anoplocephala variabilis* sp. nov.

[Figures 18-24]

This cestode has been found in *Geomys bursarius*, from Springfield, Illinois, to Emerson, Manitoba; as yet, no examinations have been made south of this region. It seems to be wholly absent from the sandhill regions; at Bemidji, Minnesota a few were found in hosts from very wet, coarse sand mixed with humus, only a foot or so from the edge of a swamp. In fertile soil, both uplands and bottoms, they vary in frequency, being in some localities extremely abundant, and in others rare or apparently absent. Not infrequently as many as fifty will be taken from a single host; in one case 136 specimens of this and a species of *Hymenolepis* were taken from one gopher. For distribution and frequency, see the table on page 62. From this table it would seem probable that the range of this species is the same as that of its host tho it is absent in many localities where its host occurs. The following description is based on well expanded specimens from central Illinois.

The total length varies from 45 to 75 mm; in life they can contract to 20 mm. or possibly less. The proglottids number from 175 to 225, the average of 19 specimens counted being 196. A neck is usually present which is four-fifths the diameter of the head, and one-half to one and one-half times as long, depending upon the stage of contraction. The strobila increases gradually in width to the posterior end, being there 2 to 3 mm. wide; occasionally the last few proglottids become narrower and longer. The first proglottids are very short. Distad they lengthen rapidly, most of the proglottids being two-thirds as long as broad. In several specimens especially in immature regions they are longer than broad. This is true only in case of extreme expansion, however. The scolex is irregularly oval in outline with sometimes a suggestion of quadrilaterality. Ordinarily it is about  $275\mu$  long by  $300$  to  $400\mu$  broad. It is distinctly set off from the neck by a deep circular groove which however is not always apparent. The suckers stand out rather prominently, due to the presence of longitudinal grooves between them, the dorsal and ventral grooves being deepest and extending farthest distad. Opposite the anterior end of the suckers the dorsal and ventral grooves arch over, the arches being as prominent as or more prominent than the suckers. These arches are the ends of a transverse bar which stands out prominently as the most anterior part of the

scolex. In frontal section this bar shows as a projecting tip in the median line. In some specimens however the bar and arches are not recognizable. The grooves never extend to the tip. The suckers open obliquely forward, at an angle of about 45 degrees from the axis of the strobila. The cuticula surrounding the orifice may be a simple fold or there may be as many as four folds of varying prominence.

The genital anlagen are represented by deeply staining cells even before strobilization is evident. The organs begin to take on recognizable form about the 45th proglottid, and eggs begin to pass into the uterus about the 75th. The genital pore is on the right margin, two-thirds of the length of the proglottid from the anterior end and considerably nearer the dorsal than the ventral surface. In some specimens it is everted during sexual activity. The cirrus pouch is  $200\mu$  long by  $75\mu$  wide, and pear-shaped. It extends well across the excretory ducts, dorsad of them. The cirrus is not spiny. Part of the vesicula seminalis occupies the median end; outside the pouch the vesicula bends upon itself twice, enlarging greatly at its inner end. From here the vas deferens takes a somewhat convoluted course across the proglottid. The testes shrink and apparently break down very early so that individual recognition is difficult. The number varies from 60 to 85; they are about  $65\mu$  long antero-posteriorly and usually somewhat smaller in other dimensions. They occur in the side away from the pore, extending from the median line to the nerve trunk and from ten to twenty lie outside the excretory ducts. They extend forward to slightly beyond the uterus and in the central part of their field entirely through the medullary portion. In expanded specimens it is clear beyond doubt that they are to be considered distal in occurrence, rather than proximal. The vaginal pore is on the ventral surface of the cloaca. The vagina lies ventral of the cirrus pouch, and at its median end usually somewhat posterior to it. Its walls are glandular. Just within the excretory canals is the receptaculum seminalis, which is at first clearly divisible into a small lateral and a larger median portion, both of which are about globular in form. Within the circle of the vitelline gland the receptaculum becomes a short, thickwalled tube, which joins the oviduct.

The ovary lies mostly to the pore side of the median line. It consists of a bar in front of the vitelline gland, turning distad beneath the median end of the latter, with lobes radiating in all directions in the longitudinal plane except directly backwards. The oviduct arises from beneath the median end of the vitelline gland mediad of the central axis of the ovary. It takes a fairly definite, sinuous course laterad, then proximad, to join the vagina. The common duct takes an irregular course to where it passes into the shell gland. The vitelline gland is a



large, horseshoe-shaped body, just to the pore side of the median line. Its duct arises from near the median line of the gland. It can be traced inside the gland as an open passage which divides and goes to the two lobes. When it has emerged from the shell gland the uterine duct passes forward and median with several windings which are fairly constant in different individuals, to join the uterus near the median line. The uterus is at first a narrow, sinuous transverse tube, just below the upper limit of the ovary and testes. At either end it crosses beyond the excretory ducts ventrally, and turns distad beyond them. Just before the eggs begin to enter the uterus expands considerably. The later development is by outpocketing, the walls of the adjacent pockets touching. The anterior pockets number 28 to 40 being usually about 35; the posterior pockets, 22 to 33, being usually about 30.

The embryo has three membranes. The outer is spherical, 30 to  $35\mu$  in diameter; the middle is loosefitting and irregular. The embryo itself is 12 to  $13\mu$  in diameter. It bears a well developed pyriform apparatus. The dorsal excretory duct lies dorsal of the ventral in young proglottids. As the proglottid ripens it passes laterad and usually ventrad also. At sexual maturity the dorsal duct is usually lateral but it may be both strictly dorsal and strictly lateral in different parts of the same proglottid. The transverse commissure is sinuous.

The foregoing description, as already stated, is based on well expanded material from central Illinois. In the material from the same localities, however, are a number of very much contracted specimens which are so different from the forms already described that they would no doubt have been classed as separate species if only the preserved specimens were known. The main differences from the type already described are as follows:

The length is 30 to 33 mm. The proglottids are all very short and broad. Mature proglottids are 0.325 mm. long by 4.5 mm. broad. The suckers open directly forward. The scolex is half-moon shaped, and is not broader than the first part of the strobila. The genital pore is situated midway on the right margin nearer the dorsal than the ventral surface. The ovary extends from the ventral excretory canal on the pore side to not far from the corresponding canal on the opposite side. The oviduct arises from the median line of the proglottid, half its length lying mediad of the vitelline gland. The transverse commissure of the excretory duct is not sinuous. The dorsal excretory duct is always lateral to the ventral, except in the head region and vicinity. In making comparisons of these two types, the reader should refer to figures 18, 19, 22, and 23.



Perhaps the most striking of these differences is seen in the position of the genital pore. This is explained however when one notes that in the elongate proglottid the portion of the body wall anterior to the genital pore lies much nearer the longitudinal muscles, and more nearly parallel to them, than does the portion posterior. As a consequence the anterior part would be shortened much more than the posterior in the process of contraction. That such is the case is shown by the fact that in contracted specimens the cuticula is much thicker anterior to the pore and is thrown into many fine wrinkles.

In order to make sure that these were really of the same species, experiments were performed with the object of trying to produce the two types at will. Complete success was attained with the simplest methods of treatment. Living specimens, just removed from the host, were cut each into two pieces; one was placed in a dish of water, the temperature of which was estimated to be about 30° C; the other in a dish of about 37°, care being taken that the portions from different worms were not confused. Those in the warmer dish soon expanded, and while in this condition they were fixed in corrosive sublimate. Those in the colder water contracted, however, and could not be induced to expand. When sectioned the portions from warm water were found to be without exception of the type first described, and those from the cold water of the second type. This simple experiment shows the necessity in comparing cestodes of taking into account the state of contraction of the proglottid.

These descriptions, as already stated, apply to specimens from central Illinois. As one passes northward, however, it is found that the individuals grow steadily smaller, both in bulk and number of proglottids. In anatomical features only one difference was discerned: the testes become very regularly fewer; apparently their size remains about the same, tho their irregular shape does not permit of exact determination on this point. The most conspicuous difference between the worms from different localities is in size, those from the north being only about half the length and breadth of those from the south. The other differences are illustrated in the following table. The numbers in parentheses indicate the numbers of individuals or proglottids examined.

Locality	Latitude	Number of Proglottids	Number of Proglottid in which Eggs first in uterus	Number of Testes
Lincoln, Springfield and Clinton, Illinois.....	40°	196 (19)	75-81 (6)	68.9 (10)
Minneapolis, Minnesota .....	45°	190.5 (2)	76 (1)	53.4 (5)
Brainerd, Minnesota .....	45° 21'	154.8 (19)	65, 68 (2)	45.5 (10)
Wahpeton, North Dakota.....	45° 21'	147 (2)	63 (1)	
Bemidji, Minnesota .....	47° 28' 30"	144.7 (3)	54 (1)	
Thief River Falls, Minnesota.	48° 7'	129 (3)	56 (1)	43.3 (7)
Emerson, Manitoba .....	49°	134.5 (2)	57 (1)	40.2 (10)

In judging from these figures it must be borne in mind that while Emerson, Manitoba is considerably farther north than Bemidji and Brainerd, Minnesota, it is, nevertheless, in the transitional zone while they are in the boreal. It will be observed from this table that while there is a considerable difference between the extremes, the intergradations are sufficiently regular to destroy the validity of these differences as specific characteristics. They are therefore here classed as one species, with the specific name "variabilis". The northern forms are further recognized as a variety, with the name *Anoplocephala variabilis borealis*.

*Anoplocephala infrequens* sp. nov.

[Figures 25 to 27]

This cestode was found rather sparingly in *Geomys bursarius* in northern Minnesota and just across the Canada line, at Emerson, Manitoba. Recently also, through Professor Ward I have received from Professor Young a cestode taken from *Evotomys* sp. at Grand Forks, North Dakota, which is identical with these. In all, ten specimens were secured from the gophers. All were taken from the last inch of the small intestine or the adjacent part of the large intestine, were unattached, and showed no signs of life. Whether or not they belong this far back cannot be said positively; but the fact that three were immature and that all but one were in good condition when found would seem to indicate that they had not died and drifted back. The following description was based upon three sectioned and three adult alcoholic specimens. Later, the specimen from *Evotomys* was sectioned and compared; no significant points of disagreement with the account here presented were discovered.

The total length is 12.5 to 20 mm. The number of proglottids is 61 to 72. There is no neck. The first proglottid is about  $40\mu$  long, and generally about five-sixths the diameter of the head. The strobila may increase rapidly in width in the first few proglottids, or the fourth or fifth may be four-fifths the diameter of the first. Mature proglottids measure 1.5 mm. wide by  $145\mu$  long. The maximum width of 2.5 to 5 mm. is reached about 7 mm. from the posterior end. Beyond this the proglottids usually narrow rapidly and lengthen somewhat. The posterior free border of each proglottid overlaps about half of the succeeding proglottid.

The scolex is 625 to  $750\mu$  broad near its anterior end. It narrows distad, passing abruptly into the first proglottid. It is nearly square in cross section with only slight indication of grooves between the suckers. On the anterior end grooves occur between the suckers, fading out just before the apex is reached. There is no indication of the circular groove found in the last species. The very large suckers open directly forward. Right and left suckers touch in the median line of the scolex, and reach very nearly to the lateral cuticula (see Fig. 26). The mouth is 70 to  $90\mu$  across. The muscular wall is 55 to  $75\mu$  thick.

The genital anlagen appear in the first proglottid. The receptaculum seminis fills in the 17th or 18th, and eggs are found in the uterus in the 21st or 22nd. The genital pores are located midway on the right margin and distinctly nearer the dorsal than the ventral surface. The cirrus pouch extends first proximo-mediad and then bends directly mediad, not enlarging beyond the bend. Its inner end lies well within the excretory ducts. The passage of the cirrus is tortuous. In the median end of the pouch is a portion of the vesicula seminalis which later enlarges to fill the entire pouch. Outside the pouch is a second portion of the vesicula. The testes shrink and apparently break down very early. They are 50 to 60 in number and are  $70\mu$  long, being usually somewhat longer than broad. Nearly all lie between the left ventral excretory vessel and the vitelline gland, but not infrequently a testis will lie wholly or in part laterad of the excretory vessel and two or three may lie dorsad of the anterior part of the vitelline gland. They extend entirely thru the medullary portion dorsoventrally.

The vaginal pore is on the ventral surface of the cloaca. The vagina lies ventrad to the cirrus pouch and partly behind it. Its walls are highly glandular. The receptacular seminis is large and elongate, reaching laterad to the ventral excretory vessel. A small part at the lateral end is indistinctly constricted off from the median portion, making it somewhat bilobed. The oviduct arises just anterior to the lower median corner of the vitelline gland and passes laterad and



proximad with several turns over the ventral surface of the latter. The vitelline duct extends as a large channel into each lobe of the gland. The uterine duct, after passing thru the voluminous shell gland, takes a crooked but regular course forward and mediad to the uterus. The very slender transverse uterus extends laterad at either end to beyond the nerve trunks. Development is by extension and outpocketing in the usual manner. The anterior pockets number 44 to 51; the posterior, 28 to 34. The ovary, in individuals from the gopher, is small, just reaching to the median line on the left, and not reaching the excretory duct on the right. In the specimen from *Evotomys*, the uterus is somewhat larger. The ovary does not cross the uterus anteriorly.

The embryo is typical. The outer membrane is usually elongate, or of other shape, due apparently to pressure. When spherical, it measures 39 to 43 $\mu$  in diameter. The middle membrane is loosefitting and irregular. The embryo itself measures 12 $\mu$  in diameter. It has a typical pyriform apparatus whose length, plus that of the embryo, is 19 to 22 $\mu$ .

The dorsal excretory duct lies laterad of the ventral. The inner duct curves very strongly laterad in the middle of the proglottid; the curve of the outer is much less. The transverse duct is sinuous in dorsoventral plane.

#### THE GENUS ANOPOLOCEPHALA

The genus *Anoplocephala* has served as a refuge for inadequately described species throughout its history. Most of the older species of the family Anoplocephalidae have been placed here at one time or another; as they have become better known, they have been removed one by one to other genera. Many of the names given have also been shown to be synonyms. Recently, von Janicki (1910), studying the cestodes from the hyrax, found that five of these supposed species did not belong even to the subfamily. Deiner (1912) has recently given an excellent and thoro description of "*Anoplocephala*" *magna* Murie; for reasons stated on page 40 I have transferred this species to the genus *Schizotaenia*. I have made the same disposal of *Anoplocephala* (*Taenia*) *gigantea*, whose anatomy MacCallum and MacCallum (1912) have recently investigated in a thoro manner.

Unfortunately, however, many of the species assigned to the genus still remain practically unknown; and more unfortunately, still other inadequately described species are being added. Thus, Mello (1912) thrusts upon the world *A. minima*, without giving any information



whatever except to external form; and Galli-Valerio (1905) burdens science with *A. dentata*, with but two lines of information as to internal anatomy and these lines devoted to non-essential details. There is no proof that either of these two species belongs even to the subfamily; and indeed, the only important fact made known concerning *A. minima*, that the genital pores are regularly alternate, indicates that it does *not* belong to the genus *Anoplocephala*.

If consideration be given to these half-starved species, no anatomical generalization concerning the genus *Anoplocephala* is possible. Thus, "*A.*" *spatula* has the testes extending across the median field; "*A.*" *omphalodes* has the genital pores irregularly alternate, the vaginal pore posterior, and the testes sometimes extending across the median field; and "*A.*" *minima* has the pores regularly alternate. For about half the species assigned to the genus, no statement whatever is made concerning the uterus. There seems no alternative, then, if one would attempt any generalizations, but to base them only on those species whose position in this genus is assured, and to ignore seeming contradictions coming from the inadequately described species which are placed provisionally in the genus.

The diagnosis of the genus should be changed so as to admit species in which the testes extend beyond the excretory ducts on the side away from the genital pore. Also, it should state that the vagina and vaginal pore are ventral to the cirrus pouch. It seems probable that in all the proximal end of the oviduct lies beneath the median lobe of the vitelline gland; but information is needed concerning more species on this point.

The diagnosis of the genus *Anoplocephala* thus becomes as follows.

*Anoplocephalinae*, with segments generally much broader than long, occasionally longer than broad. A single set of reproductive organs in each segment. Genital pores unilateral. Genital canals pass on the dorsal side of the longitudinal excretory vessels and nerve. External vesicula seminalis present. Testes on the side away from the genital pore, sometimes extending laterad of the nerve trunk. Vagina and vaginal pore ventral to the cirrus pouch. Female glands to the pore side of the median field. Uterus a transversely elongated sac, with pocket-like appendages, anteriorly and posteriorly. Eggs with well developed pyriform apparatus. Adults in mammals.

Type-species: *Anoplocephala perfoliata* Goeze 1782.

The following species may be assigned with certainty to the genus *Anoplocephala*.

<i>A. perfoliata</i> Goeze	<i>A. magna</i> Abildgaard (syn., <i>A. plicata</i> & <i>A. zebrae</i> )
<i>A. globiceps</i> Diesing	<i>A. mamillana</i> Mehlis
<i>A. wimerosa</i> Moniez	<i>A. variabilis</i> Douthitt
<i>A. infrequens</i> Douthitt	

The following species are not well enough known to allow of generic determination, but should be left here for lack of better disposal.

<i>A. inermis</i> von Linstow (syn., <i>A. arvicolae</i> )	<i>A. blanchardi</i> Moniez <i>A. dentata</i> Galli-Valerio
<i>A. omphalodes</i> Hermann	<i>A. paronai</i> Moniez
<i>A. restricta</i> Railliet	<i>A. spatula</i> von Linstow
<i>A. transversaria</i> Krabbe	

*Schizotaenia americana* Stiles 1895

[Figures 28, 29]

Stiles in 1895 gave a short description of this cestode and placed it in the genus *Andrya*. The next year he transferred it to the genus *Bertia*, (now *Bertiella*). In 1906 von Janicki, having proposed the genus *Schizotaenia*, included this form and *Bertiella americana leporis* in that genus, basing his action mainly upon the distribution of testes, since the description of Stiles was noncommittal or erroneous on other points that might be of importance. The results of the present studies justify completely von Janicki's disposal.

In 1906 Cohn expressed it as his opinion that this cestode was the one described by Leidy (1855) as *Taenia laticephala*, and that the specific name "*americana* Stiles" should be dropped as a synonym. I cannot agree that the evidence justifies such a conclusion. With full consideration for the ability of cestodes to contract and expand, it is a severe strain on one's credulity to conceive how a cestode 1.3 inches long and 2.8 lines broad could at will become 9 inches long, and  $\frac{3}{4}$  of a line broad; and how a proglottid 12 times as broad as long could become square. Moreover, Leidy states that the width of the neck in the forms at his disposal is  $\frac{1}{4}$  of a line, or one-half the diameter of the head. These specimens have no neck and strobilization is very conspicuous even in the first proglottids. Leidy states that the anterior proglottids are oblong-square. If this means that they were longer than broad, we have a condition that is unprecedented in the *Anoplocephalidae*; if it means that they were broader than long, then Leidy's speci-

mens must have been composed of at least 225 proglottids, more probably of 350 or 400 proglottids.

The fact that Leidy's and Stiles' material were from the same host, the only point that Cohn seems to have taken into consideration, means nothing. I have taken 16 species of cestodes from *Geomys*, and have not exhausted the field; Stiles (1896) has reported still another. These species represent seven genera, and three families. The balance of evidence seems to be in favor of Stiles' view that Leidy's species was a species of the genus *Davainea*.

Cohn criticise Stiles for the inadequateness of his description; but with sectioned material before him he failed to add anything of importance to our knowledge. Incidentally he mentions that the female glands are situated at a considerable distance from the median line, which proves that he did not have before him Stiles' species but had probably *Schizotaenia variabilis*, the next species discussed in this paper.

There were available for study specimens from Stiles' material loaned by the Bureau of Animal industry; others were placed at Professor Ward's disposal by Professor M. J. Elrod, the original collector of the material; also, from the Bureau of Animal Industry a specimen from a porcupine taken at Mayfield, Michigan. The first lot is from *Erethizon epixanthus*, from Snake River, Wyoming; the second is from *Erethizon dorsatus*. I have also specimens (No. 1502, B. A. I. Coll.) identified by Stiles as this species; examination has shown that they are distinct.

External form (Stiles (1896))—"Strobila attains 33 mm. in length by 6 mm. in breadth and contains about 90 segments, the oldest of which are 8 mm. long. Head unarmed, measures 0.6 mm. broad by 0.38 mm. long by 0.32 mm. thick, and is nearly rectangular in apex view. The neck is absent, and the head is frequently retracted in the body, as in *Drepanidotaenia lanceolata*. Suckers round, 0.176 mm. in diameter, open anteriorly".

The genital organs alternate, in the specimens at hand, with perfect regularity from right to left. The genital anlagen are visible in the first proglottid. The specimen from Mayfield, Mich., shows the 70th proglottid still immature; apparently, maturity is reached about the 80th. No other specimen at hand gave information as to this point. One must conclude from this condition, either that Elrod's material was all immature since it shows the total number of proglottids to be about 90, or that the species is larger when inhabiting *Erethizon dorsatus*. The latter conclusion seems more probable, since some of the detached proglottids of the Elrod material are ripe.



The genital cloaca could not be studied as carefully as desired, on account of its habit of turning inside out at the approach of sexual maturity. A full comparison of the organ with that of *Schizotaenia anoplocephaloides*, to be described later, is therefore not possible. They agree however in all points that could be made out. In both the cloaca everts at the approach of sexual maturity; and in both it is drawn back at the close of sexual activity, but in none of the sectioned material at hand does it come back completely. In both the cloaca is very large tho in the present species it is not so extraordinarily large as in the other. The proglottids sectioned do not show whether the cloaca is divided into two parts, as in *S. anoplocephaloides*. The pore is located about midway on the margin.

The cirrus pouch is quite large, tho small as compared with that of *S. anoplocephaloides*. When the cloaca is not everted, about a third of it lies mediad of the excretory ducts; when everted it reaches usually just to the nerve trunk. It is 500-625 $\mu$  long by 185-210 $\mu$  wide. It is somewhat pear-shaped in outline, the inner half being about uniform in diameter. Laterad of the middle it tapers sharply to end in a slender neck 40 $\mu$  in diameter and 150 $\mu$  long. The cirrus is spiny. Extruded cirri however are smooth, from which it would seem that the attachment of the hooks is very light. This probably explains the apparent absence of spines observed by Stiles for *S. americana leporis*. The inner end of the cirrus pouch is occupied by a portion of the vesicula seminalis. Outside the cirrus pouch the vesicula is about 80 $\mu$  in diameter in mature proglottids and extends mediad and proximad for a distance of about 850 $\mu$ , coming to lie here near the anterior end of the proglottid. It then curves usually to extend mediad and distad for a distance of about 225 $\mu$  where it ends in the slender vas deferens. The vasa efferentia are in a large part plainly visible. The vesicula seminalis if closely examined is seen to be somewhat sinuous; but the effect is that of a straight tube taking the course mentioned. At its extreme inner end just at this juncture with the vas deferens it has glandular walls. The testes are spherical and 65 $\mu$  to 80 $\mu$  in diameter. They are all dorsal and extend from excretory duct to excretory duct in the distal end of the proglottid. The number was found to be about 70 which agrees with the account of Stiles.

The vagina and vaginal pore are anterior to the cirrus pouch. For about the first 185 $\mu$  of its length the vagina is a very small, heavy-walled tube which is perfectly distinct when once recognized. Beyond this point it is very indistinct and usually can be traced only by the vacuolated appearance of its course. In a few cases, however, it can be seen very indistinctly anterior to the cirrus pouch, crossing the



vesicula seminalis just beyond the pouch and then proceeding mediad to the receptaculum seminalis. Just before entering the receptaculum it again becomes distinct. Thus in position only does it resemble the conspicuous, glandular vagina of *S. anoplocephaloides*. The rather small, nearly globular receptaculum seminis lies just anterior to and laterad of the vitelline gland partly overlapping it.

The female glands are but slightly displaced from the median line. In proglottids 4 to 5 mm. wide the median axis of the shell gland is  $55\mu$  to  $175\mu$  distant from the median line. The female organs of the right and left sides therefore overlap largely. The transverse diameter of the ovary is about 1.3 mm. It is composed of a transverse portion in front of the vitelline gland from which numerous small lobes radiate in all directions except towards the vitelline gland. To either side of the vitelline gland the lateral portions turn distad and extend to near the transverse commissure of the excretory duct. The ova measure  $12\mu$  to  $15\mu$  in diameter. The oviduct is short; its attachment to the ovary is located anterior to the central axis of the vitelline gland. This latter gland is of the regular Anoplocephaline form, being composed of a small lateral and a large median lobe. Here, however, is a clear approach to the peculiar mulberry-like form found in the next species and in *S. hagmanni*. The two lobes approach each other anteriorly, thus restricting the space between them and making the gland more compact and show an indication of the division of the gland into many small radiating lobes. The transverse diameter of the gland is  $400\mu$ . The shell gland is  $90\mu$  in diameter; it needs no further description.

The uterus in the earliest stages observed is a continuous sheet of tissue extending through nearly the whole of the median field, except for the portion occupied by the ovary and vitelline gland. The two lateral portions are connected by a narrow strip above the ovary. There is abundant indication of thickening of the uterine tissue into definite lines, thus simulating a network such as is found in *Moniezia*. These do not develop into open tubes, however, so it is not really a reticulum. For a discussion of this type of uterus see under *S. anoplocephaloides*. The condition of the material unfortunately does not permit the development of this organ to be worked out in full detail. In its fully developed stage it is divided up into a great many small compartments, each containing several eggs, similar to the condition described later for *Moniezia expansa*. It seems, therefore, that the uterus does not break down into egg-capsules after the manner of the Linstowinae, but that the condition is due to unequal development of the original cavity at different points. In its fully developed stage the uterus is practically confined to the median field but a small branch extends out to occupy

the vacuolated space surrounding the cirrus pouch. The fully developed uterine embryos are  $14.5\mu$  to  $15.5\mu$  in diameter. The inner embryonic membrane is  $18\mu$  to  $20\mu$  across; the length of the embryo plus the pyriform body is  $26.5\mu$  to  $29\mu$ . The outer membrane is  $55$  to  $61\mu$  in diameter; the middle is loosefitting and irregular.

The ventral excretory duct has a diameter of  $45$  to  $75\mu$ , and the dorsal is about half this size. Both lie in approximately the same dorsoventral plane. Near the distal end of the proglottid the ventral duct turns and runs abruptly mediad for a distance of about  $275\mu$  where it gives off the transverse commissure. Beyond the commissure and therefore in the next proglottid the duct turns laterad not so abruptly as before to regain its lateral position. Stiles records that he has observed the dorsal duct in open communication with the transverse commissure; since this occurs also in *S. variabilis* and *S. anoplocephaloides*, it seems to be a common occurrence in the genus.

Stiles in 1896 referred to this species five cestodes from a rabbit (host species and locality not known), giving them the rank of a variety with the name *Bertia americana leporis*. His description is very unsatisfactory being based upon poorly preserved, unsectioned material. In reading over carefully the description of the worms there does not appear a single anatomical character upon which to justify giving them the rank of a distinct variety. The cirrus is supposed to be smooth; but this conclusion is based upon extruded cirri, and as shown, extruded cirri of the forms from the porcupines are usually if not always smooth. The testes are stated to be probably fewer; but Stiles is not certain as to the count and the difference moreover is not so great as that between the extremes of the next species. The description of the position of the genital pore is vague but implies a difference; yet his figures (Stiles 1896, Pl. X, Figs. 7, 14, and 15) are identical for both. Some slight differences were observed in the first appearance of the genital anlagen; but such appearances when based upon unsectioned specimens and poor material, do not have any importance. No other points of difference were brought out which could not be accounted for as mere individual variations. There appears therefore to be no evidence to justify giving these specimens the rank of variety.

On the other hand there is very little evidence that these cestodes rightly belong to this species, or even to the genus for that matter. As will be shown in the succeeding paragraphs the supposedly homogeneous materials from the porcupine prove to be two distinct species. Until something is known of them however they should not be given separate recognition.

*Schizotaenia variabilis* sp. nov.

[Figures 30 to 32]

Some years ago Dr. A. K. Fisher collected cestodes from a number of porcupines (*Erethizon dorsatus*) at Lake George, New York. These in the Bureau of Animal Industry at present bear serial number 1502. Stiles (1896) examined them and identified them as *Bertia americana* (now *Schizotaenia americana*). Professor Ward secured the loan of these specimens. Examination has shown that they do not represent *S. americana*, but are a distinct species. The following description is based upon a single complete specimen, not sectioned, and several sectioned portions from the region of sexual maturity. The specimens reported by Cohn (1906) from *Erethizon epixanthus* from Alaska seem referable to this species rather than *S. americana*, since he reports that the female glands are located far from the median line.

The complete specimen at hand, which appears to be fully grown and has shed proglottids, is 20 mm. long and is composed of 60 proglottids. The greatest width, 8.5 mm., is reached 18 cm. from the head; back of this the strobila narrows somewhat. All the proglottids are very short in comparison with the width, except the last which is 6 mm. wide and 1.5 mm. long. The fragments at hand agree with this specimen, except that some have longer and thicker proglottids the width being the same; this would seem to indicate that they came from a larger specimen. Three scolices are present; they measure  $450\mu$  long by  $875\mu$  wide. One is retracted within the end of the strobila as in *S. americana*.

The genital pores are regularly alternate. The genital cloaca and cirrus pouch agree with the description just given for *S. americana*, except that the cirrus pouch is somewhat smaller being ordinarily  $485$  to  $500\mu$  long tho it is sometimes longer. Its width is  $140$  to  $185\mu$ . The vesicula seminalis is of necessity much shorter than in *S. americana* on account of the nearness of the female glands to the lateral margin. It is variable in form, being sometimes straight and sometimes in the form of large, wide loops, as shown in Fig. 30. The gland-cells on the inner end of the vesicula are usually more numerous than in *S. americana*, as shown in the same figure. The vagina is identical but of course shorter.

The testes are decidedly unlike *S. americana* in form and distribution. Nearly all are elongated anteroposteriorly, the breadth being to the length as  $5:7$ . In some specimens they are  $60$  to  $80\mu$  long while in others they are  $95$  to  $130\mu$  long. These measurements were all taken at sexual maturity. They occur only in the median field and are



mostly on the pore side of the median line of the proglottid. Beyond the median line they are reduced to a single row which reaches as far as the median axis of the female glands of the proglottids before and behind. On the pore side of the field they are in  $2\frac{1}{2}$  to 5 rows when viewed from above. They are usually limited to the dorsal part of the proglottid but in one specimen they sometimes extend entirely through the medullary portion. Generally they lie almost entirely posterior to the female glands, but in one specimen they were found sometimes at the same level as the female glands and dorsal to them, and in some proglottids even anterior to them, and therefore if judged by position in the proglottid in front! These different types of distribution were all found in five adjacent proglottids. The number of testes was found to vary from 60 to 70 in one specimen to 110 in another. The number seems to be fairly constant for any given individual.

As already stated the genital organs alternate regularly from the left to the right side of the strobila. The median line of the female glands in mature proglottids is  $600\mu$  from the median line of the proglottid; in *S. americana* the distance was 55 to  $175\mu$ . The ovary is much smaller than in *S. americana*, its diameter varying from 650 to  $900\mu$ ; it never reaches to the median line of the proglottid. Otherwise the ovary is not different from that of *S. americana*. The ova measure 12 to  $14\mu$  in diameter. The vitelline gland shows the peculiar mulberry-like appearance figured by von Janicki for *S. hagmanni*. In cross sections of the gland, i. e., longitudinal sections of the proglottid, about 25 radiating lobes can be made out. There is no trace of the usual bilobed condition. The shell gland is small and lies directly dorsad of the vitelline gland, having about one-third the diameter of the latter. The uterus in mature proglottids is apparently not so extensive as in *S. americana*, but statements concerning it must be qualified on account of the poor condition of the material. It does not seem to reach either the anterior or the posterior border of the segment. Otherwise, the description given for *S. americana* will apply equally well for the early stages. Unfortunately the later development could not be followed.

The description given for the excretory system of *S. americana* will answer for what seems to be the normal condition here. One individual however offers such radical departures from this type that a detailed description is given here. In the specimen in question the longitudinal portions of both dorsal and ventral ducts are of approximately the same size. In one sectioned portion having five proglottids, the large ventral transverse commissure extends laterad to make open connection also with the dorsal duct. Judged by its appearance, the commissure would seem to belong to the dorsal rather than



the ventral system in these cases, and the connection with the ventral system appears secondary. This effect is heightened by another remarkable feature, the presence of a secondary transverse commissure anterior to the first. This duct is a direct continuation mediad of the longitudinal ventral duct at the point where the latter dips distad just before communicating with the main transverse commissure. This secondary duct is usually of small diameter dorsoventrally but antero-posteriorly it may extend through one-fourth the length of the proglottid. Its diameter however is very irregular, and its course is sinuous. These secondary commissures are apparently analogous to the condition found in *S. anoplocephaloides*. The connections between dorsal ducts and transverse commissures were observed also in *S. anoplocephaloides*, and by Stiles in *S. americana*. In two proglottids the main transverse commissures are not fully developed, but are represented by strings of disconnected spaces. This may be due however to the fact that the proglottids are not quite mature. All these conditions are illustrated in Fig. 31.

*Schizotaenia anoplocephaloides* sp. nov.

[Figures 33 to 40]

Four gophers (*Geomys breviceps* Baird) from creek bottom land at Norman, Oklahoma, yielded of this species plentifully. About half of the 75 specimens taken were lost and tho many others are not in the best condition, some are good. For distribution and frequency of this species see the table on page 62.

The total length of the specimens at hand is 30 to 33 mm. The number of proglottids varies from 55 to 80, the average being 68. There is no neck. The first proglottids are about seven-tenths the diameter of the scolex and from one-eighth to one-twelfth as long as broad. The maximum width of 1.7 to 2 mm. is reached about the middle of the strobila; back of this the width remains constant or decreases slightly. At the middle of the strobila the proglottids are from one-fifth to one-third as long as broad. They increase in length as they become older, becoming finally two-thirds as long as broad. In those proglottids in which the eggs are being fertilized the large everted genital pore protrudes prominently.

The scolex averages  $390\mu$  in diameter and  $320\mu$  long and is quite distinct from the strobila. It is clearly separated into anterior and posterior portions by a slight transverse constriction near its middle. The apex is blunt, the anterior outline being a regular curve. The scolex is rather deeply four-lobed owing to the presence of longitudinal

grooves between the suckers, the dorsal and ventral grooves being the deepest. All four fade out before reaching the apex. The very prominent suckers face anterolaterad at an angle of about 45 degrees from the axis of the worm. The mouths of the suckers are from 25 to 40 $\mu$  in diameter and the cavities are 70 to 90 $\mu$  deep. The muscular wall of the sucker is from 25 to 50 $\mu$  thick.

There is one set of reproductive organs to the proglottid, these alternating with practically perfect regularity from right to left; in a dozen worms examined only three cases were found of two adjacent proglottids with pores on the same side. The anlagen of the female glands can be made out in the first proglottid. Testes are to be recognized in the 15th and eggs pass into the uterus in the 40th. The genital cloaca presents an unusual appearance. It is clearly divisible into two parts, a lateral and a median. The lateral is an unusually large structure varying in shape in different specimens probably on account of contraction from nearly globular to angular, being even acutely angular at its inner end. The pouch has a length of about 140 $\mu$  and a breadth of about 85 $\mu$ . The anlage of this structure can be made out in about the 20th proglottid as a group of cells that stain deeply. Soon afterwards a mass of substance not distinguishable from the cuticula can be made out in it near the lateral margin. A lumen appears which increases in length mediad and then expands. Just before sexual maturity the cuticula of the outer body wall is broken through, and the cavity of the pocket becomes continuous with the outer surface. The pouch immediately turns inside out, projecting abruptly in some cases for more than 200 $\mu$  from the margin. Fifteen or twenty proglottids farther back it is again retraced to remain thus to the end. In its fully developed stage the cuticula and wall of the pocket are directly continuous with the cortical layer and not distinguishable from it. Mediad of this and communicating with it is a second small pocket. It is rather small and is expanded at its inner end to embrace the end of the cirrus pouch. The vagina opens into its anterior border. Generally, the median end of the cloaca lies mediad of the longitudinal excretory ducts.

An unexpected condition was found in the position of the vagina and cirrus pouch with respect to each other and to the nerve and excretory trunks. When the pouch and vagina are on the right margin of the strobila they cross the excretory ducts dorsally; but when on the left, in two individuals out of ten studied, they more often cross the excretory ducts ventrally. In these two individuals out of 19 proglottids which had the pores on the left margin ten had the genital ducts ventral. Thus some proglottids have an arrangement that is charac-

teristic of the Linstowinae and has been observed nowhere amongst the Anoplocephalinae, except possibly in the genus *Triplotaenia*. It should be stated however that the identification of right and left sides in these specimens may be in error.

Still another interesting feature was observed in regard to the genital ducts. The vagina crosses the cirrus pouch ventrally in most cases; but in the two individuals mentioned in the paragraph above, 12 of the proglottids that had the excretory ducts dorsal to the genital ducts, had the vagina dorsal and the cirrus pouch ventral. This recalls at once *Moniezia* in which the vagina is regularly ventral to the cirrus pouch on the right and dorsal on the left. These same two individuals were unusual in the form of the ovary, as explained below. The cirrus pouch is very large. Before the evagination of the cloaca it lies usually entirely mediad of the excretory ducts; but when the cloaca is everted it may lie entirely laterad. In mature proglottids it is 275 to 370 $\mu$  long, and 120 to 240 $\mu$  broad. Before the development of the vesicula seminalis it may be elongated and spindle-shaped; afterwards it is always pear-shaped. The cirrus is straight in the lateral half of its length and has usually two spiral turns at its upper end. It is lined with many hundreds of small hooks which are arranged in spiral rows. The median end of the cirrus pouch is occupied by a portion of the vesicula seminalis. Proximad and mediad of the pouch is a second portion, 140 $\mu$  long, which is only slightly coiled. This portion is thickly beset with glandular cells. Beyond the seminal vesicle the passage narrows and soon divides, sending a branch to either testicular field.

The testes, 70 to 110 in number, are dorsal and posterior. They occur in both lateral halves but are mostly on the side away from the pore. At either side they are grouped two or three deep dorsoventrally. Above the yolk-gland there is never more than a single layer and as often as not there are none here, the testes being separated into two groups. The testes are typically spherical in shape, averaging 35 $\mu$  in diameter.

The vagina communicates with the genital cloaca on the anterior surface of the latter. It extends forward and somewhat mediad in front of the cirrus pouch then turns directly toward the median line, usually crossing the cirrus pouch ventrally. Mediad of the cirrus pouch it curves somewhat distad, the entire vagina thus describing a semi-circle. Its middle portion in the anterior part of the proglottid is several times the diameter of the two ends. The surface is glandular. At about the same level as the lateral end is located the receptaculum seminis which is a simple expansion of the vagina, measuring 180 by



130 $\mu$ . The ovary is distinctly, but not considerably, to the pore side of the median line. It is fanshaped in outline, being formed of a large central mass from which about 30 lobes radiate extending in all directions in the horizontal plane except towards the part of the field occupied by the vitelline gland. It is distinctly ventral in position. In two specimens however most of the proglottids which have the genital pore on the left side have the ovary separated into distinct dorsal and ventral portions with a narrow connection between them. The dorsal portion in these cases is of about half the area of the ventral and thin. These are the individuals that show the peculiarities of the excretory ducts already mentioned. The oviduct in all cases connects with the ovary at a point directly in front of the vitelline gland and is short. The vitelline gland is of the ordinary bilobed type which is found nearly everywhere in the subfamily and shows no suggestion of the type found usually in the genus. It lies posteriorly to the ovary, sometimes extending dorsad to the cortical layer and dividing the testes into two fields. In cross section it is distinctly horseshoeshaped, with the open face dorsad. Viewed from above it is U-shaped but with the median arm much larger.

The uterus is first recognizable as a sheet of deeply staining cells ventrad of the testes and dorsad of the ovary. Just beneath the margin of each testicular field the sheet is thickened into a heavy circular band. On the pore side there extends forward from the anterior tip of the circular band a strip of the same nature, which crosses the vagina laterad of the receptaculum seminis then turns and extends diagonally distad just underneath the anterior margin of the receptaculum and anterior to the vitelline gland. It joins with the other circular band at the corner of this gland. It is into this cross duct that the uterine duct empties. Within these circles and anterior to the transverse portion and connecting with them at frequent points, is a network of strands formed by thickenings of the uterine tissue which recalls strongly the reticulate uterus found in *Moniezia*. The transverse portion is of course the first part of the uterus to receive eggs; but the eggs pass immediately into the circular bands which have developed into canals. The extreme lateral portions fill and then the whole canals. As the uterus fills with eggs these passages expand centrally and the transverse portion anteriorly, so that the cavity of the uterus becomes one continuous sac. The extension from this stage is by regular outpocketing no different from that found in *Anoplocephala* and *Bertiella*, except that the pockets are of necessity shorter since the uterus does not begin as a simple tube. The development of the uterus continues until nearly all the organs of the proglottid are reabsorbed. The cirrus pouch and



vesicula persist to the last either in situ or crowded to one side. The receptaculum persists as a mere vestige. The shell gland persists as a structureless mass connected with the receptaculum and with the posterior end of the proglottid by a narrow bridge, such as has been described for *Moniezia carrinoi* and some of its relatives. All the other organs are reabsorbed, the testes being the last to give way. The proglottid becomes little more than a thin-walled egg capsule, the cortical layer being reduced sometimes to a thickness of  $20\mu$ .

The uteri of the three species of *Schizotaenia* here described agree in all essential respects but differ decidedly from the account presented by von Janicki (1906) for *S. hagmanni* which is accepted as the type of the genus. He recognized nothing comparable to the degenerate reticulum or diffuse uterus described here; also the three species described here show nothing comparable to the "äusserst feinen Schlitz, der als mannigfach gewellte Fläche durch den grössten Teil der Markschicht \* \* \* \* sich hinzieht". Von Janicki does not figure this structure except in transverse section, in which way it gives very little information. In view however of the fact that such a structure would not be greatly different in appearance from that of the degenerate reticulum described here, I am inclined to believe the difference is one of interpretation rather than structure. Likewise von Janicki's drawings of the "Spaltenwerk" (Figs. 85, 86) resemble closely the condition observed in frontal sections of the early saccular stage when the thin uterus is applied to the uneven surface of the ovary and only parts of the cavity appear in each section. There is no ground therefore for considering these uteri as differing fundamentally in this regard. The possession of uterine outpocketings by the present species is striking and is significant as to its relationships; but the fact offers no barrier to its inclusion in the genus *Schizotaenia*; it is what should be expected in the more primitive members of the genus.

The uterine embryos have three membranes. The outer is spherical and 30 to  $40\mu$  in diameter. The middle is loose-fitting and irregular. The diameter of the embryo is 10 to  $17\mu$  with no considerable range of variation in any one individual. There is a perfectly developed pyriform apparatus whose length plus that of the embryo is 16 to  $26\mu$ . The two stout tapering horns cross at the tip and extend backwards as long, slender processes.

The excretory ducts lie in about the same dorsoventral plane, the originally dorsal duct outside. This arrangement is present in both strobila and scolex. The path across the proglottid is a curve. The dorsal duct is usually between 10 and  $12\mu$  in diameter at the ends of the proglottids, narrowing in the middle to 6 or  $7\mu$  on the side away

from the pore, and on the pore side to  $3\mu$ . The ventral duct at the ends of the proglottids is  $40$  to  $50\mu$  in diameter; it narrows in the middle to  $30$  to  $35\mu$  on the side away from the pore, and on the pore side to  $3$  by  $10\mu$ . The transverse commissure of the ventral duct is a straight tube  $25$  to  $40\mu$  in diameter. In three individuals the dorsal longitudinal duct is connected with the transverse commissure in very many cases (Fig. 40). In the present species these connections are always on the same side of the strobila, judged to be the right side, tho since the specimens are in longitudinal sections this could not be determined finally.

In the anterior aporose portion of the proglottid the transverse commissure becomes divided and with the aid of the main duct surrounds an "island" of medullary parenchyma which varies from  $60$  to  $200\mu$  long and may have its long axis either longitudinal or transverse. From this region but varying considerably in point of origin a large branch duct extends distad and mediad into the proglottid. This duct persists after the uterus is fully formed, projecting free into its cavity and invested by its walls. Frequently a similar duct will extend forward from the transverse commissure in the lower pore corner of the proglottid.

There appears to be no doubt but that this cestode is most nearly allied to the genus *Schizotaenia*. Yet it shows very clearly that it is related to the genus *Anoplocephala* and appears to be transitional between the two. Aside from the close general resemblances between the two genera the following characters show its close relationship to the known representatives of the genus *Anoplocephala*.

1. The testes are mainly on the side away from the pore.
2. The vitelline gland is of the type found in *Anoplocephala*, and shows no suggestion of the type occurring in most other known *Schizotaenia*.
3. The uterus develops by regular anterior and posterior out-pocketing.
4. The cirrus pouch is unusually large.

#### THE GENUS SCHIZOTAENIA

Deiner (1912) has published an account of the anatomy of *Taenia magna* Murie 1870, under the name *Anoplocephala latissima*, the specific name "*magna*" being dropped because preoccupied by *A. magna* Abildgaard 1789. The account is very thoro and bears all the marks of being strictly dependable. A consideration of the anatomical features leaves no doubt whatever in my mind but that this cestode is a true repre-

sentative of the genus *Schizotaenia*. Briefly summarized, the following points brought out by Deiner support this conclusion.

1. The testes are mainly on the pore side; this agrees with some *Schizotaeniae* and disagrees with all known *Anoplocephalae*.
2. The cirrus is spiny.
3. The vagina and vaginal pore are anterior to the cirrus pouch.
4. The structure of the vagina is identical with that of *S. anoplocephaloides*.
5. The oviduct connects with the ovary directly in front of the vitelline gland.
6. The uterus, while relatively simple, shows clearly a resemblance to *Schizotaenia*.

These features are all characteristic of the representatives of the genus *Schizotaenia*. Some of them are found nowhere else; none of them are found in any species known to belong to the genus *Anoplocephala*. In one character only does this cestode resemble *Anoplocephala*: the genital pores are all dextral. This character however can not be considered to outweigh the other anatomical resemblances and the cestode is therefore placed in the genus *Schizotaenia*.

MacCallum and MacCallum (1912) have published a careful account of the anatomy of *Taenia gigantea* Peters 1856, usually referred to the genus *Anoplocephala*. This cestode also shows marked affinities for *Schizotaenia* and while the case is not so strong as in the other, the evidence is sufficient to indicate the position of the cestode. The evidence that *Taenia gigantea* Peters is a *Schizotaenia* follows.

1. The testes are mostly on the pore side.
2. The cirrus is spiny.
3. The vagina was not observed. Since the investigators expected to find it posterior to the cirrus pouch, an inconspicuous and transitory vagina, such as is found in *S. americana* and *S. variabilis*, anterior to the pouch might easily have been overlooked.
4. The vitelline gland is lobulated.

*Taenia gigantea* Peters is therefore here transferred to the genus *Schizotaenia*. Its specific distinctness from *S. magna*, long disputed, seems assured.

With six of the species of *Schizotaenia* well known it is now possible to judge the value of the various anatomical features much more satisfactorily than could von Janicki, who had before him but one that was satisfactorily described. It becomes evident that several of the characteristics he proposed must be restated and several others show themselves to be of generic rank. In making such generalizations the poorly



known *S. decrescens* should not be given serious consideration. Its position in the genus is not assured and the statements concerning it are not clear-cut and dependable. The conception of the genus must be changed in the following particulars:

1. The testes do not necessarily extend "von Längsgefäß zu Längsgefäß" in the distal part of the proglottid. They may be in two lateral groups, or all on the pore side, and they may be mostly anterior.

2. In the main the genital canals "ziehen dorsal an den beiden Excretionsgefäßen und dem Nervenstrang vorbei"; yet recognition must be given to the fact that the opposite may be the case in some proglottids.

3. The position of the vagina and vaginal pore anterior to the cirrus pouch is an absolute distinction from all other known genera of the subfamily and indeed from nearly all known cestodes, and should have recognition as perhaps the most important generic character. The unsatisfactory description of *S. decrescens* is noncommittal but gives no information opposed to the conclusion that the vagina is anterior here also.

4. The union of the oviduct with the ovary in all sufficiently known species of the genus is located directly anterior to the middle of the vitelline gland. This fact should be stated in the diagnosis.

5. The diagnosis should state that cirrus is spiny.

Accordingly the genus *Schizotaenia* should be characterized as follows:

Anoplocephalinae, with segments broader than long. Genital pores regularly alternate or dextral, and in one doubtful species irregularly alternate. Dorsal excretory duct lateral of ventral. Genital canals pass usually dorsal of longitudinal excretory vessels and nerve, tho the reverse condition has been observed. Testes confined to the median field, either distal in position or proximal, and mostly on the pore side. Cirrus pouch very large and muscular, cirrus spiny. External vesicula seminalis present. Vagina and vaginal pore anterior to the cirrus pouch. Female glands placed towards the pore side of the median field. Oviduct joins the ovary directly in front of the middle of the vitelline gland. Uterus not a simple transverse tube, usually perhaps always a degenerate reticulum; confined to the median field in anlage, and in its fully developed stage either there or crossing the excretory ducts mostly on the dorsal side. No pyriform apparatus. Adults in mammals.

Designated as type: *Schizotaenia decrescens* Diesing 1856.



The genus *Schizotaenia* embraces the following well described species.

*Magna* group: Genital pores dextral. Testes mostly anterior and mostly on the pore side. Size of known species enormous.

*S. latissima* Deiner

*S. gigantea* Peters

*Hagmanni* group: Genital pores alternate. Testes posterior. Known species small.

*S. hagmanni* von Janicki

*S. variabilis* Douthitt

*S. americana* Stiles

*S. anoplocephaloides* Douthitt

"*Schizotaenia*" *decrescens* (Diesing 1856) Lühe 1895, which von Janicki unfortunately designated as the type of the genus, seems to belong to this group and should be treated as such until better known. "*Anoplocephala*" *transversaria* shows some of the characteristics of this group but not enough information is accessible to justify a change of position.

#### THE UTERUS OF MONIEZIA EXPANSA

The cestodes of the genus *Moniezia* have received more attention than those of any other genus of the family. As a result of the studies of Stiles and Hassall, Tower, Fuhrmann, and a number of other workers, most of the points of anatomy have been determined carefully. Strangely enough, however, practically no attention has been given to the uterus except to observe that it begins usually as a reticulum; one is left to assume that the later development is not different from that of related forms. My own observations however have tended to show that the development of the uterus is in many ways unique and furnishes hints as to the relationship of the genus. I had for study several specimens of *Moniezia expansa*, taken from sheep at Lincoln, Nebraska, and belonging to the collection of Professor Henry B. Ward. No observations at variance with accepted anatomical accounts were made so structures other than the uterus have not been taken up, except that a drawing of a mature proglottid is included for comparison (Fig. 41).

The uterus in *Moniezia expansa* begins as a reticulum (Fig. 42), whose slender branches are quite distinct and lie at a considerable distance from each other. It extends nearly the whole length of the proglottid in the space that lies between the shell glands. Beyond these glands on either side two branches, occurring respectively in the anterior one-third and the posterior one-third of the proglottid, extend laterad to beyond the excretory ducts on the dorsal side of the latter. Upon the entrance of the eggs the cavities of the various branches of the uterus enlarge somewhat. The eggs come to lie in bunches which are distributed equally to different parts of the proglottid. As the

embryos develop the portions of the uterus containing these bunches expand. This expansion continues until the enlarged spaces fill almost the entire medullary portion, the tissue substance between the different regions of enlargement being reduced greatly in thickness but remaining to the last to separate these chambers from each other (Fig. 43). In no stage does the uterus force its way between the excretory ducts and the ventral cortical layer. Thus here in the ripe uterus is a condition that is very unusual in the Anoplocephalinae, and which indeed has been observed in only one other species of the group, namely, *Schizotaenia americana*. One recalls at once the uterus of the Linstowinae, tho there is no indication that the uterus ever really breaks down in the present species. It appears therefore it would not be correct to speak of the compartments as egg-capsules in the sense that the term is used, even tho it is probably a step in that direction.

Drawings by Stiles and Hassall (1893) of gravid uteri of *Moniezia planissima* and *M. alba* indicate structures which, tho not so represented, may be identical with the walls of the compartments found in *M. expansa*. There is a slight indication of such structures also in their drawing of the gravid uterus of *M. neumanni*. Their drawing of *M. trigonophora* shows no such structures but since they give no indications of such structures in their drawing of *M. expansa*, the absence means nothing. Thus no evidence available is opposed to the conclusion that the Monieziae from mammals have the uterus similar in all essential respects to the condition here described for *Moniezia expansa*. The excellent account of Fuhrmann (1902) shows however that the uteri of the Monieziae from birds differ in almost every point from the type just described. The difference between these two groups, if the condition for *M. expansa* is likewise the condition for other mammalian Monieziae, may be summed up as follows:

<i>Monieziae from mammals</i>	<i>Monieziae from birds</i>
Mature uterus crossing excretory ducts	Mature uterus not crossing excretory ducts
Mature uterus a complicated reticulum	Mature uterus a simple transverse tube, or with a few simple branches
Gravid uterus in the form of many separated or nearly separated compartments	Gravid uterus saccular, or with simple anterior and posterior pockets
Embryos with pyriform apparatus, the horns of which end in disk	Embryos without pyriform apparatus
Dorsal excretory duct median to ventral	Dorsal excretory duct dorsal to ventral

Diamare (1900) who was first to give more than mention of the Moniezia from birds, created the genus Paronia for the species he was considering (*Moniezia carrinoi*). His conclusions, however, were not based upon a sufficient knowledge of the cestodes in question or the Anoplocephalidae in general, and Fuhrmann very properly included this cestode and other related ones which he described in the genus Moniezia. If, however, the additions here made to the knowledge of *Moniezia expansa* should hold true for the other Moniezia from mammals, there seems to be little question but that the genus Paronia should be revived for the forms from birds. It would be rash to conclude, however, that the other Moniezia from mammals agree with *M. expansa* in this regard. If one considers the different members of the genus Schizotaenia, one finds as great a diversity in uterine structure as is here exhibited. As to the other differences noted, they are not by themselves sufficient reasons for the separation of the genus Moniezia, since other Anoplocephalid genera show both conditions for each structure. Any division of the genus Moniezia would seem premature, therefore, without first examining several species. Consideration of this step is left to some worker who has access to such material.

For reasons stated on page 49 I have transferred Zschokke's "*Moniezia*" *diaphana* to the genus Cittotaenia. Von Janicki's description of *M. beauforti* is not accessible to me; but since it is an avian parasite, it is here considered as belonging in the *carrinoi*-group. I can not find evidence to support Parona's action in placing *Taenia frontina* (Dujardin 1845) in this group. Until something more is known of this cestode it should by all means be left where it will do no harm. The genus Moniezia as here accepted includes therefore the following species:

- |                                           |                                 |
|-------------------------------------------|---------------------------------|
| 1. <i>Carrinoi</i> -group                 | <i>M. columbae</i> Fuhrmann     |
| <i>M. carrinoi</i> Diamere                | <i>M. variabilis</i> Fuhrmann   |
| <i>M. ambigua</i> Fuhrmann                | <i>M. beauforti</i> von Janicki |
| 2. <i>Expansa</i> -group                  |                                 |
| <i>M. expansa</i> Rudolphi                | <i>M. neumanni</i> Moniez       |
| <i>M. trigonophora</i> Stiles and Hassall | <i>M. alba</i> Perroncita       |
|                                           | <i>M. amphibia</i> von Linstow  |
| <i>M. oblongiceps</i> Stiles and Hassall  | <i>M. rugosa</i> Diesing        |
|                                           | <i>M. festiva</i> Rudolphi      |
| <i>M. planissima</i> Stiles and Hassall   |                                 |
| <i>M. benedeni</i> Moniez                 |                                 |

Apparently in all Moniezia the oviduct connects with the ovary directly in front of the vitelline gland and the uterus crosses the excre-



tory ducts dorsally or not at all. These points should be stated in the diagnosis of the genus.

The diagnosis therefore becomes as follows:

Anoplocephalinae, with segments generally broader than long. Two complete sets of reproductive organs in each segment, or with but one continuous uterus. Uterus generally reticular, either confined to the median field or crossing the excretory ducts dorsally only. Oviduct joins with ovary directly in front of the middle of the vitelline gland. Genital canals cross on dorsal side of longitudinal excretory vessels and nerves. Interproglottidal glands often present. Vagina ventral and cirrus dorsal on right side of the proglottid; the reverse on the left side. Pyriform apparatus present or absent; when present, the horns end in a disk. Adults in mammals and birds.

Type-species: *Moniezia expansa* Rudolphi 1810.

#### THE CITTOTAENIAE OF NORTH AMERICAN RABBITS

There have been described and named as parasites of North American rabbits four Cittotaeniae, namely, *C. perplexa*, *C. mosaica*, *C. pectinata*, and *C. variabilis*. Of *variabilis* I had at hand the material studied by Lyman (1902) and several specimens I collected at various points in Kansas and Oklahoma. The observations confirm Lyman's statements and need be discussed no farther. A drawing is given (Fig. 44) for purposes of comparison.

Of *C. pectinata* there is at hand Lyman's material from Kansas and Nebraska and also two individuals which I collected at Neosho Falls, Kansas. I have been unable to find any confirmation of Lyman's statement that the uterus in anlage extends beyond the excretory ducts. Stiles (1896) and Hall (1908) also conclude that it does not. In some instances I have observed that the fully developed uterus extends slightly beyond the excretory ducts dorsally; but usually it is confined to the median field at all stages. Lyman states that the greatest diameter of the lobes or pouches of the ovary is  $16\mu$ . My own measurements of Lyman's material and my own show a diameter of 40 to  $60\mu$  as the usual condition. Since the ova themselves are 15 to  $18\mu$  in diameter his figures seem most probably a typographical error.

The specimens taken at Neosho Falls, Kansas, are in some respects quite different from Lyman's. The testes are practically absent from the middle part of the proglottid and somewhat more numerous in the lateral parts than in Lyman's material. These two specimens which have shed some proglottids are 45 mm. long and consist each of 85 proglottids. Lyman's specimens were up to 71 mm. long and had when



complete 110 to 140 proglottids; Stiles' material measured up to  $400\mu$  long. Eggs begin to pass into the uterus in the 45th proglottid in one of my own specimens. My measurements of the heads of the two specimens show diameters at the base of 700 and  $745\mu$  respectively but confirm Lyman's measurements for the specimens he studied. There seems no reason to doubt Stiles' figures which give the diameter of the head as  $250\mu$  or less. These different figures show little reliance is to be placed upon these characters.

In certain features the American representatives of this species are different from the European and should be designated as a distinct variety to avoid confusion. The following is the characterization.

*Cittotaenia pectinata*: Strobila up to 400 mm. long. Sexual maturity about 30 mm. from the anterior end. Testes about 150, extending uniformly across the distal end of the proglottid, from excretory duct to excretory duct. Hosts *Lepus timidus* and *Lepus variabilis*. Known distribution, Germany and France.

*Cittotaenia pectinata americana*: Strobila 44 to 71 mm. long. Number of proglottids, 85 to 140. Sexual maturity reached in about the 45th proglottid, about 10 mm. from the anterior end. Testes 100 to 125, extending from excretory duct to excretory duct in the distal end of the proglottid, sometimes nearly absent from the median part of the field. Host, *Lepus californicus melanotus*. Known distribution, eastern Kansas and Nebraska, U. S. A.

Of *Cittotaenia perplexa*, I have studied U. S. National Museum cestode No. 1110, which is one of the specimens upon which Stiles (1896) based his original description and which was designated by him a cotype. Permission was given to dismount and section the specimen. Inasmuch as it had been mounted in balsam for 18 years, this was obviously a difficult task to accomplish; but by careful work two series of sections have been made, which, while by no means suited for careful study, are sufficient to show that all the differences supposed to exist between this cestode and *C. mosaica* (Hall, 1908) are due to errors or incorrect conclusions as to the former. These points will be taken up one at a time.

The cirrus pouch Stiles (1896) records as being 288 to  $320\mu$  long in *C. perplexa*. Eighteen pouches I measured, however, were all  $530\mu$  long. Hall found the pouch in *C. mosaica* to be 475 to  $640\mu$  long, with an average length of  $550\mu$ . There is therefore no difference in this regard. In position and form the cirrus pouch and vagina are identical with Hall's descriptions. The specimen at hand is not suited for histological study and comparison. According to Stiles' description the testes of *C. perplexa* are absent from the median part of the pro-

glottid. In the specimen at hand, however, they extend across the field continuously in a manner identical with the description by Hall for *C. mosaica*. There is of course no reason to doubt the correctness of Stiles' observation; but it seems evident that the condition he described is not diagnostic. As mentioned, I have found the testes in *C. pectinata* almost separated in two fields.

Hall recognizes in his specimens some differences from Stiles' account as to the time of first appearance of genital organs. He acknowledges that such differences may be due to differences in technique and mentions that Stiles' account was based upon unsectioned material. I have not attempted to section the anterior end of the specimen at hand since it is not in condition for close study. However there is no valid reason for considering the specimens different on this point. The mosaic markings mentioned by Hall can hardly be considered of importance; anyway, they are shown to a slight extent by the specimen at hand.

There are no other points of difference between the two accounts. I have compared Stiles' cotype in nearly every particular with Hall's account and find only two points of difference: (1) eggs appear first in the uterus in the 94th proglottid; and (2) the ovary is  $850\mu$  across, and of somewhat different appearance from the condition Hall describes. These points of difference are taken up in the paragraph after the next.

Specimens of this form from cottontails (*Sylvilagus floridanus*) at Blair, Oklahoma, show the ovary exactly as described by Hall and of the same dimensions, that is, about  $600\mu$  across. The cirrus pouch is somewhat smaller, and old pouches, when gorged with sperm, shorten up and become pearshaped. In two specimens sexual maturity is reached in the 90th proglottid. In other points they do not differ from Hall's description. Figures 46 to 49 are from this material. These Oklahoma specimens, it will be seen, resemble the Maryland specimen in that maturity is reached about the 90th proglottid. The gorging and shortening up of the cirrus pouch suggests an explanation of the basis of Stiles' measurements. The general appearance of the worms is identical with both the Maryland and the Colorado forms, and the form of the ovary is identical with that of those from Colorado. It seems very probable that the appearance of the ovary presented by the Maryland specimen is due to the flattening process to which it was subjected preparatory to mounting in toto. The lobes stretching out laterally at full length are in just the position they would assume with such treatment. As to the difference in the stage at which maturity is reached, the same explanation would apply here as for *Anoplocephala*

*variabilis* (page 22). Bowie, Maryland, and Blair, Oklahoma, are in the Upper Austral faunal zone, while Seven Lakes, Colorado, is in the Boreal.

The Colorado forms may deserve the rank of a separate variety, on account of the difference in stage of sexual maturity; but until the character has been determined for more than two or three individuals on each side, such a step would not be justified. Variations of far greater import have been recorded in this paper which were found in individuals of the same species and from the same host, and even in different proglottids of the same individual. The name, *Cittotaenia mosaica*, should therefore be dropped, and the excellent description by Hall (1908) applied to *C. perplexa*, the only change necessary being to recognize that sexual maturity may not occur until the 95th proglottid and that in addition to occurring in *Sylvilagus pinetis* of Colorado it also occurs in *Sylvilagus floridanus* of Maryland and Oklahoma. There seems no reason to doubt that the testes are sometimes separated into two groups, as described by Stiles.

*C. pectinata* and *C. perplexa* are strikingly similar in several unique characters, and it seems not improbable that their differences may be due to environmental conditions, since one is a parasite in the cottontail and the other in the jack rabbit; but my present opinion is that such a decision would be premature, without testing it by breeding experiments. *C. perplexa* differs from *C. pectinata* in the following points, all of which are quantitative:

1. The testes are fewer
2. The cirrus pouch is smaller
3. There is a more complicated network of excretory ducts in the lateral portions of the median field
4. The ovary is smaller

#### THE GENUS CITTOTAENIA

Zschokke in 1907 described a cestode from *Phascolomys wombat*, giving it the name *Moniezia diaphana*. His excellent description however seems to be that of a perfectly normal *Cittotaenia*, and disagrees with *Moniezia* on every point in which these two genera differ. The species is here transferred to the genus *Cittotaenia* for the following reasons:

1. The vagina is not ventral on the right and dorsal on the left, as in *Moniezia*.
2. There are no shields on the ends of the horns of the pyriform body.



3. The uterus is tubular—not reticular.

4. The dorsal excretory duct is dorsolateral to the ventral.

Two changes should be made in the diagnosis of the genus *Cittotaenia*. It should be stated that the oviduct joins the ovary directly in front of the median axis of the vitelline gland and that the uterus crosses the excretory ducts dorsally only, or not at all.

The diagnosis therefore becomes as follows:

Anoplocephalinae, with segments broader than long. Two sets of reproductive organs in each segment. Genital canals pass dorsal of longitudinal excretory vessels and nerves. Interproglottidal glands absent. Vagina ventral of cirrus pouch on both sides of the segment. Oviduct joins ovary directly in front of the median axis of the vitelline gland. Uterus either confined to the median field or crossing the excretory ducts dorsally only. Development usually by simple anterior and posterior outpocketing. Eggs with well developed pyriform apparatus of ordinary type, or without pyriform apparatus. Adults in mammals and birds.

Type-species: *Cittotaenia denticulata* Rudolphi 1804.

The genus *Cittotaenia* includes the following species, most of which are fairly well known:

1. *Marmotae*-group. Cirrus pouch pyriform, distinct. Dorsal duct lateral or dorsal of ventral (no statement concerning *C. bursaria*).

<i>C. marmotae</i> Braun	<i>C. praecocquis</i> Stiles
<i>C. denticulata</i> Rudolphi	<i>C. ctenoides</i> Railliet
( <i>C. latissima</i> Riehm	<i>C. diaphana</i> Zschokke
( <i>C. goezei</i> )	<i>C. zschokkei</i> von Janicki
<i>C. bursaria</i> von Linstow	<i>C. quadrata</i> von Linstow

2. *Pectinata*-group. Cirrus pouch much elongated, resembling nozzle of a hose, and indistinct; becoming pyriform occasionally in old proglottids. Dorsal excretory duct median to ventral.

<i>C. pectinata</i> Goeze (in part)	<i>C. rhea</i> Fuhrmann
<i>C. variabilis</i> Stiles	<i>C. psittacea</i> Fuhrmann
( <i>C. mosaica</i> Hall)	<i>C. avicolae</i> Fuhrmann
<i>C. perplexa</i> Stiles	<i>C. kuvaria</i> Shipley

## COMPARATIVE STUDIES ON THE ANOPOLOCEPHALIDAE

Fuhrmann's classification of the Cyclophyllidea (1907) which is accepted here recognizes in the subfamily Anoplocephalinae the genera *Triplotaenia*, *Cittotaenia*, *Moniezia*, *Anoplocephala*, *Andrya*, *Bertiella*, *Schizotaenia* and *Aporna*. Each of these genera is well defined and



distinct; and except for *Triplotaenia* and *Aporina* they form a compact and orderly group. But little attention has been given to the relationships of these genera to each other. In the following pages the various resemblances in the different organs are considered, with reference to the question of relationships between the various genera.

1. *The Structure of the Uterus*.—Two general types of uterus have been recognized in this group: the tubular, found in *Bertiella*, *Anoplocephala*, and most *Cittotaeniae*, and the reticular, found in *Andrya*, most *Monieziae*, and some *Cittotaeniae*. In addition the uteri of *Schizotaenia*, *Triplotaenia*, and *Aporina* have been recognized as each being a distinct type in itself, tho the uterus of *Triplotaenia* is not really different from the tubular. The uterus of *Schizotaenia* has been shown in this paper to be of the reticular type, the reticulum being apparently in the process of degeneration. There appears no reason to regard the uterus of *Aporina* as of any other than the tubular type. As to the relationships of the reticular and tubular types to each other, very little has been done in the way of investigation except to conjecture. Generally the reticular type has been supposed to be derived from the tubular by the outgrowth and anastomosis of proximal and distal branches. Following are offered the conclusions from studies of the reticulate uteri of different species of *Andrya*, made with the view of studying the relationships of these two types to each other.

In the earliest stages in which indications of the uterus were observed it occupies the entire region later occupied by the fully developed reticulum. This stage is long before any lumina appear. The uterine tissue is more or less diffuse, there being no indication of segregation along lines, except that it is more or less "stringy" in transverse axis. As the proglottid increases in size, the cells segregate more and more into definite lines which run in all directions and connect at frequent intervals, forming a network. These lines of segregation do not spread from any central locality but appear *in situ* and so far as could be observed, at about the same time in all parts of the proglottid. Later cavities appear in these tubes; these again do not spread out from any central source but appear *in situ* and without the stimulus of entering ova. When fully developed they form a continuous network of open tubes. As these tubes become filled with ova they expand and coalesce, forming a single saccular cavity. Development then proceeds by regular outpocketing, anteriorly and posteriorly. Thus in the early stages of development there is no indication that the reticulate uterus has been derived from a transverse tubular type by outgrowth and anastomosis of branches, as was suggested by Stiles (1896). It is true of course that the uterus spreads from some original source in the course

of development; but there is no evidence that there intervenes a transverse tubular stage which is comparable in any sense to the uterus of Anoplocephala.

On the other hand it seems much more probable that the reticulate uterus has been derived by lateral spreading from a median longitudinal uterus, such as we find in more primitive cestodes, and is the first step in the evolution of the transverse uterus rather than the last; that the tubular uterus of Anoplocephala has been the product of simplification. Schizotaenia seems to be in an intermediate condition; the uterus appears in a widely diffused condition but the cavity appears first as an anterior transverse tube. Some such view becomes necessary if Andrya is regarded as a primitive type, as other characters indicate. It is a matter of sincere regret to me that other matters prevent making a careful study of the uterus at this time.

Aporina, Andrya, and Anoplocephala agree in that the uterus, in nearly all species, extends laterad beyond the excretory ducts, crossing them ventrally. Never does it cross them dorsally in anlage and at all stages it lies mostly ventral. In Schizotaenia, and apparently always in Bertiella, it is confined to the median field in mature proglottids and in its fully developed stage crosses the ducts mostly on their dorsal side, if at all. In Cittotaenia and Moniezia the uterus in anlage usually crosses both excretory ducts dorsally but in some species is confined at all stages to the median field. Apparently it never penetrates between the excretory ducts and the ventral cortical layer. These points furnish very important indications of the relationships of the varied genera to each other. The development of the uterus by outpocketing must be recognized as a very general character of the subfamily, and in general, a primitive one. It has been shown to be the method of development in Andrya, where it was supposed not to occur, and in one species of Schizotaenia.

2. *The Distribution of Testes.*—The genus Aporina has been considered unique in that the testes extend laterad beyond the excretory ducts. In the present paper however are described four species of Andrya and two of Anoplocephala in which the testes do extend across the excretory ducts on the side away from the pore, and in the other species of Anoplocephala here taken up they do in many proglottids. Likewise, Zschokke's figures for Bertiella edulis (1899, Taf. XX, Fig. 2) shows that in this species the testes may extend nearly across the ducts. It seems probable that they occur in the lateral fields in all or nearly all species of Anoplocephala and Andrya, and in the median field in all species of Schizotaenia and most species at least of Bertiella. The double pored genera of course, cannot be compared in this regard.

The genus *Aporina* remains distinct in that the testes cross the excretory ducts on the side in which the pore would be, if one were present.

The testes of *Bertiella* and most species of *Andrya* are anterior; those of *Andrya* occupy almost the entire median field except for the space above the ovary. Those of most species of *Schizotaenia* and at least some species of *Anoplocephala* are mainly posterior; and for *Cittotaenia* and *Moniezia* they are posterior in all cases where one can judge. However, *Andrya translucida* has the testes posterior and two species of *Schizotaenia* have them mainly anterior. It is therefore impossible to form any final conclusions as to the paths of evolution in this regard. In looking however for the type that has the most generalized distribution of testes, attention is at once attracted by the conditions found in *Andrya*. Here, especially in *Andrya primordialis*, is found a near approach to a distribution that could give rise by suppression to any distribution found in the subfamily, with the exception of *Aporina*.

3. *The Vaginal Pore and Vagina*.—The position of the vagina and vaginal pore with reference to the cirrus pouch appears from these studies to be the most stable generic character. In *Aporina* and *Andrya* the vaginal pore and vagina are directly posterior to the cirrus pouch, which position is primitive among cestodes. In *Bertiella* the pore and vagina are either posterior or somewhat dorsal. In *Anoplocephala* the pore is ventral to the pouch, and the vagina is ventral, and for at least the lateral half of its length is not posterior. In *Cittotaenia* the pore and vagina are ventral but may be at the same time posterior also. In *Moniezia* they are ventral to the pouch on the right side and dorsal on the left and usually they are also somewhat posterior. In *Schizotaenia* both vagina and vaginal pore are directly in front of the cirrus pouch. The evidence provided here points to the conclusion that the three genera first mentioned are the most primitive.

4. *The Ovary*.—Two types of ovary can be distinguished. In one the lobes radiate in all directions in the horizontal plane from the point of attachment of the oviduct; in the other the lobes radiate from a transverse bar, which forms the basal part of the ovary. The second type is perhaps the only one found in *Anoplocephala* and *Schizotaenia*, and it is present with modifications in *Moniezia* and *Cittotaenia*. The first type is typically represented in *Andrya*. Unfortunately most of the drawings of species of *Bertiella* and *Aporina* are obscure on this point. At any rate the character is not of much systematic importance because the two conditions are not very distinct from each other and are obscured by modifications.

5. *The Excretory ducts*.—Nothing is known as to the excretory ducts of *Triplotaenia*. *Bertiella* and *Moniezia* have the dorsal ducts



either dorsal or dorsomedian, and *Cittotaenia* has them dorsal, lateral or dorsomedian. Usually the dorsal duct is lateral in *Anoplocephala* and *Schizotaenia*; but in certain stages of contraction it has been observed to be directly dorsal in both genera. In *Andrya* the dorsal duct is lateral in all cases observed. In the scolex of all species of *Andrya* and *Anoplocephala* which were observed however, the dorsal duct is dorsal while in *Schizotaenia anoplocephaloides* it is lateral in the scolex. It would appear therefore that little evidence as to relationship is provided by the excretory ducts.

### THE EVOLUTION OF THE ANOPLOCEPHALIDAE

The following arguments favor the conclusion that *Andrya* approaches most closely of all the genera to the ancestral type of the Anoplocephalidae.

1. In *Andrya* the ovary is either median, or very close to the median line, and none of the female glands are far from the median line.

2. In *Andrya* the vagina and vaginal pore are directly posterior to the cirrus pouch.

3. In *Andrya* is found the most generalized distribution of testes, with the possible exception of *Aporina*.

4. In the generalized species of *Andrya* is found a primitive, unmodified vas deferens, which character is found in no other genus except *Aporina*.

5. In *Andrya* is found the most genuine and least modified reticulate uterus.

6. In *Andrya*, the uterus in anlage, crosses the excretory duct ventrally.

As characters of more doubtful value, the following may be noted.

1. The pyriform body is simple (no pyriform body in *Aporina*).

2. The vesicula seminalis is, in the most generalized species, a simple, globular expansion.

3. The genital pores are in some species irregularly alternate.

As specialized characters of *Andrya* I can see but one; the genital pores are either dextral or tend towards dextrality, whereas one would expect the ancestor of the Anoplocephalidae to have single, irregularly alternating genital pores. Such a point constitutes but a slight departure however in the light of the different arrangements that have arisen in the family; and in this regard evolution could easily reverse its action. The possession of a prostate gland would seem at first to be a specialized character; but this structure appears to be associated with



an unmodified vas deferens and to cease to have a purpose for existence when the vas deferens comes to function as a storehouse for spermatozoa, as is the case in all other genera except *Aporina*.

Within the genus *Andrya* there has been a wide range of evolution. *A. primordialis* is decidedly the most primitive in structure of ovary and uterus and testicular distribution; and only in the arrangement of genital pores is it unlike what should be expected in the ancestors of all the Anoplocephalidae. In *Andrya macrocephala* and *A. translucida* on the other hand is found a rather high degree of specialization. As regards position in the scale *Aporina* is a close contestant with *Andrya* for the most primitive position, each having distinct points in its favor. *Aporina* must be regarded however as an offshoot since certain characters which it possesses exclude it from the direct line.

From forms like the most primitive *Andryae* there sprang apparently a line destined to give rise to all the other Anoplocephalidae, except possibly *Bertiella*. The characteristics of this line, many of which were subsequently modified, were as follows:

1. The lobes of the ovary did not radiate from the point of attachment of the oviduct, but instead extended out from a transverse bar which formed the base of the ovary.

2. The vagina and vaginal pore had begun to move anteriorly and ventralwards.

3. The testes had come to lie mostly in the posterior part of the proglottid.

4. The cirrus pouch had begun a conspicuous development in size, foreshadowed in *Andrya primordialis*.

5. The female glands remained in the primitive position, near the median line.

6. The prostate gland was lost and the vesicula seminalis was acquired.

The genus *Anoplocephala* apparently separated from the rest early, and developed along somewhat different lines. It retains the following *Andryan* characters.

1. The uterus, in anlage, crosses the excretory ducts ventrally.

2. The testes extend into the lateral field on the side away from the pore.

3. The proximal end of the oviduct lies beneath the median lobe of the vitelline gland.

4. The tendency towards dextral arrangement of genital pores is retained and perfected.

After Anoplocephala had split off the common line became modified as follows:

1. The uterus ceased to cross the excretory ducts, in anlage.
2. The ovary moved forward and laterad so as to lie directly in front of the vitelline gland with the proximal end of the oviduct in front of the median line of this gland.
3. The testes become confined to the median field.

From this line developed Cittotaenia, Schizotaenia, and Moniezia. Cittotaenia resembles Anoplocephala in some respects but the following evidences of relationship to Moniezia outweigh them:

1. In both, the uterus crosses the excretory ducts dorsally only, never ventrally as in Anoplocephala, Andrya, and Aporina. In some cases in each of these two genera, the uterus is confined to the median field at all stages.
2. At least one Cittotaenia has a reticulate uterus.
3. Both have two sets of genital organs.
4. The dorsal excretory duct is dorsal or median to the ventral in most species of each.

The points arguing for close relationship between Moniezia and Schizotaenia are as follows:

1. Each retains at least remnants of the reticulate uterus.
2. Some individuals of Schizotaenia show asymmetry in regard to the relations of the genital glands.
3. Moniezia has, to a considerable extent, at least, the mulberry-like vitelline gland, such as is found in most species of Schizotaenia.
4. The ripe uterus is divided into compartments in some species of both genera.

Although retaining the reticulate uterus Moniezia and Schizotaenia are in many ways the most specialized representatives of their subfamily, except of course for Triplotaenia. They have specialized along different lines and the decision as to which is nearest the ancestral line depends upon the criteria adopted.

The position of Bertiella in this scheme is somewhat doubtful. I had no specimens at hand for study and so must depend upon the accounts of others. The following points argue for close relationship with the higher representatives of the genus Andrya rather than with other genera.

1. The vagina and vaginal pore are directly posterior, or posterior and dorsal to the cirrus pouch.
2. The cirrus pouch is either identical with the higher Andryae

in form and size, or much smaller (the pouch is larger in the other genera).

3. The testes are mainly anterior.

4. In species concerning which information is available, the oviduct and ovary are related to each other as in *Andrya*, and not as in *Schizotaenia*.

The following points argue for relationship rather to *Schizotaenia*-like forms, however.

1. The cirrus is sometimes spiny.

2. The genital pores are sometimes regularly alternate.

3. The uterus, at least in anlage, is confined to the median field.

4. The dorsal excretory ducts are often dorsomedian, as in relatives of *Schizotaenia*.

5. The testes seem to be confined to the median field, as in *Schizotaenia*; in some species of *Schizotaenia*, also, the testes are anterior.

I am inclined to consider the arguments for closest relationship to the genus *Andrya* as the most important, and to attribute the resemblances to *Schizotaenia* to parallel evolution.

The relationships of the genus *Triplotaenia* are problematical and will probably always remain uncertain. The possession of two sets of reproductive organs suggests relationship to *Cittotaenia* or *Moniezia*. The following points argue for relationship to *Schizotaenia*.

1. The uterus, in anlage, is confined to the median field.

2. The horns of the pyriform body are long and filamentous.

3. The vagina is inconspicuous and apparently ephemeral.

These points argue for little more than general relationship however and all of them might easily be accidental.

The following points argue that *Thysanosoma* is most nearly related to the higher representatives of the Anoplocephalinae and is descended from forms like *Moniezia* and *Schizotaenia*.

1. There are sometimes two sets of reproductive organs in *Thysanosoma*.

2. The genital ducts sometimes cross the excretory ducts ventrally in *Schizotaenia*.

3. The genital organs are placed far laterad, in *Thysanosoma*.

4. The vaginal pore may be dorsal, or anterior to the cirrus pouch, in *Thysanosoma*.

5. Accessory transverse commissures of the excretory ducts are present in species of both *Schizotaenia* and *Thysanosoma*.

These arguments however are at best inconclusive. The most that can be said is that *Thysanosoma* seems to be related to the higher Anoplocephalinae.



That *Stilesia* and *Avitellina* are quite closely related to *Thysanosoma* is too evident to need discussion. The exact position of these genera with respect to each other must be left unsettled, however, until the species of *Thysanosoma* have received more careful study. At present we can do no better than accept Gough's decision (1911) that *Stilesia* and *Avitellina* represent a subfamily distinct from *Thysanosoma*.

In the subfamily Linstowinae, conditions are unsettled and uncertain, owing to the recent efforts of Beddard (1911, and 1912), and others. It seems little short of absurd to decide from external characters (1911:652) as to which of about 20 genera a given cestode should be referred to, the possible list including such genera as *Anoplocephala*, *Zschokkeella*, *Thysanosoma*, *Davainea*, *Hymenolepis*, *Oochoristica* and *Taenia*. Within two years, Beddard has actually placed one cestode (whose latest name is *Zschokkeella gambianum*) in three genera, representing two subfamilies; and there is no assurance that the present disposal is final. Since Beddard has proved his worth as an investigator by his researches in other fields, one might expect better things in the future; but as yet, while he has dwelt at great length upon the significance of the size and appearance of sucker and scolex, the presence or absence of a neck, and other such features, he has failed to tell, in any instance, whether the genital ducts cross the excretory ducts dorsally or ventrally, or pass between them; at least, several hours were spent in search in his voluminous articles without finding any information on this point. Bischoff (1912) has likewise contributed considerably towards a state of general confusion in this group. He has added to the genus *Inermicapsifer* several species, without giving, apparently, any adequate study to each. The few facts that he gives are not sufficient in most cases to show that the species exist; and if they do exist, there is no evidence in many cases that they should be placed in the *Inermicapsifer* group rather than in some allied group.

In the present condition of affairs, there are no characters except trivial unimportant ones upon which to separate the so-called genera *Zschokkeella*, *Inermicapsifer*, *Thysanotaenia* and *Hyracotaenia* from each other. My own opinion is that they all belong in one genus, with the exceptions of *Zschokkeella remota* and *Thysanotaenia lemuris* which seem to belong elsewhere. In the present condition of our knowledge of most of the species of the group, however, any alterations would merely add to the confusion already existing. "*Taenia*" *anoplocephaloides* must be given a place amongst the Linstowinae, close to the genus *Linstowia*. Of the genera of the Linstowinae, *Linstowia* shows, by the



position and form of genital organs and excretory ducts, that it is the most generalized, unless "*Taenia*" *anoplocephaloides* be given a lower place. The following facts argue that *Linstowia* is descended from the higher Anoplocephalinae, from forms somewhat like *Schizotaenia* and its relative *Moniezia*.

1. The uterus, in some *Schizotaenia* and *Moniezia*, in its fully developed stage is divided up into compartments much like the embryo-capsules of the *Linstowinae*.

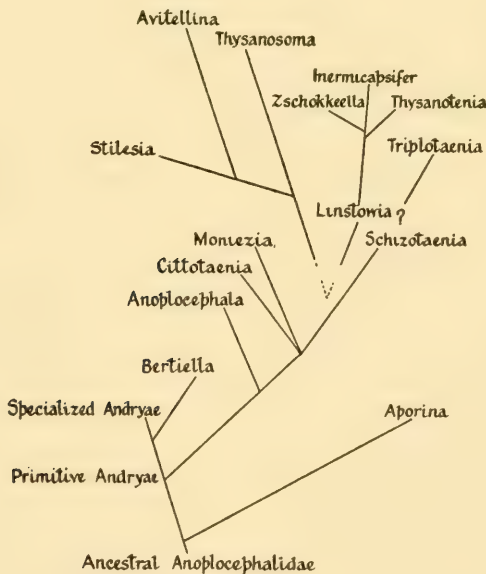
3. The uterus of the *Linstowinae*, in anlage, is not different in type from the diffuse uterus of the genus *Schizotaenia*.

3. The uterus apparently crosses the excretory ducts dorsally in the *Linstowinae*; information is vague or wanting as to most species, however.

4. The genital ducts have been observed to cross the excretory ducts ventrally in some individuals in *Schizotaenia*.

5. The cirrus pouch is unusually large in *Schizotaenia* and *Linstowia*.

The following diagram represents the scheme of evolution here proposed.



## LIFE HISTORIES OF POCKET GOPHER ANOPOLOCEPHALIDS

Throughout the present studies attention has been given to the problem of the life-histories of the cestodes of the pocket gopher. This problem has been attacked in three ways: by experimental feeding, by examination of suspected hosts for cysticercoids, and by observations on the habits of the gopher. Either the first or second method, or both, have been tried out on all the parasites and commensals of the gopher which I have been able to find, with only negative results as yet; it is my intention to keep steadily at this quest whenever opportunity offers. Observations on the habits of the gopher however have yielded information which may prove of decided value in the quest of the intermediate hosts of the Anoplocephalidae, and this information is given here in the hope that the facts may be of assistance to other workers who are giving attention to this subject. In order to make the matter clear a brief statement is necessary concerning the habits of the gopher.

I have found *Geomys personatus* always in infertile, sandy ground. *Geomys breviceps* I have caught at various points in Texas and Oklahoma; but nowhere except at Norman, Oklahoma, have I caught them in anything except upland regions in very sandy soil. At Norman, gophers were taken along a stream valley in soil that is of a sandy nature but fertile and moist. *Geomys bursarius* I have found to range over about every conceivable locality. They thrive on the borders of swamps, on hilltops, on open plains, in heavy pine forests, in wind-blown sand, and in heavy clay soil, whether uplands or lowlands.

Wherever he occurs, the gopher leads a life wholly apart from his fellows except at the mating season. His tunnel is seldom as much as 50 meters long. This tunnel is practically the gopher's world except during the mating season. In the evening he may come to the top of the ground for a few moments; but he does not wander more than a few feet from the mouth of the burrow. In regard to the occurrence of all the species of Anoplocephalidae found infesting the gopher, one rule has proved to be invariable: they occur only in gophers inhabiting rich soils, preferably clay soils, but occasionally in sand when it is mixed with humus and is of a swampy nature. To this rule I have found not a single exception. Apparently not all regions of fertile soil are infected, and lowlands in the main are most heavily infected. Swampy places have been found to yield the best of all.

A specific instance is illuminating. At Brainerd, Minnesota, fifteen gophers were caught in the sandhills; on examination one cestode was found which belonged in the genus *Hymenolepis*. The traps were then moved to Bean Flat, 200 meters away. Bean Flat is a low, almost

swampy region in which the gophers can live only along the margins of the low river terraces which cross the flat. With a single exception, every adult gopher examined was infected, this locality and another 200 meters away which was similar yielding five species of Anoplocephalid cestodes of three genera. Twenty-six specimens, representing three species, were taken from one host. When one considers that the gopher never wanders more than a few feet from the mouth of his burrow except during the mating season this fact becomes all the more significant. The conclusion is forced upon the student that there is some connection with the nature of the soil that determines the infection; it seems most probable that the intermediate hosts are plant-feeding insects that live only in fertile soil preferring wet lowlands.

Since this rule holds true for six species of four genera of the Anoplocephalidae it seems probable that it will hold true for the family generally; that there is something associated with fertile soils and swampy places that is necessary for the continued existence of these parasites; that if cattle and sheep could be confined to sandhill pastures (which assuredly would not be practical), they would not become infected with *Thysanosoma* and *Moniezia*. This rule is at least worth trying out by other workers who are giving attention to the life-histories of these cestodes. The camel cricket (*Ceuthophilus*) has been found to abound in the tunnels of the pocket gopher in localities where these cestodes occur and to be absent from localities where the cestodes do not occur. However all attempts to infect these animals have resulted in failures. It is my intention to continue these experiments both with these animals and others whenever opportunity offers.

The following table shows the infections found in adult gophers. All gophers that were less than 8 months old, even tho fully grown were without exception uninfected. The separation of the various species of *Hymenolepis* which were found was rather hastily done and only approximate correctness was aimed at. The species of *Cittotaenia* from Brainerd, Minnesota, was unfortunately immature and could not be worked out. It is not *C. praecocquis* described by Stiles (1896) from the same host-species. The examinations were all made by me, with the exception of those from Nebraska for which I have to thank Dr. John E. Gutberlet.





## KEY TO KNOWN SPECIES OF ANOPLOCEPHALIDÆ

Owing to the fact that the literature of this group is scattered, uncoordinated, and often inaccessible, the task of identifying material is often very difficult and time-consuming. The writer in taking up for the first time the several groups here studied, has had good cause to realize this. In the hope that it will spare to others this waste of labor in becoming acquainted with the field, the following key to all the known species of Anoplocephalidae is presented. A great many poorly described species are represented here, species as to whose affinities no one has any means of judging. In order to avoid confusion they are left in the genera to which they have been assigned, tho in many cases there is no proof that they belong even in the family. To prepare a key for such species has been found very difficult and in some cases the only thing that could be done was to list them with such descriptions as are possible.

In order not to hamper the serviceableness of the key only the more important synonyms are given and usually only the best reference is given for each species. For an exhaustive bibliographic account of the various species and genera, the reader is referred to Stiles & Hassall's excellent summary (1912). True phylogenetic characters have been used wherever possible; and wherever such exist, classifications previously proposed have been accepted. No attempt has been made to treat the Linstowinae critically; they are included here merely to make the key complete and critical study is left to someone better fitted to take up the work.

Family Anoplocephalidae: Scolex and suckers unarmed. Segments nearly always broader than long, generally many times broader than long. Genital pores marginal (absent in *Aporina*). Testes numerous, except in *Triplotaenia*. Uterus transverse. Embryos with thin, transparent shells, usually with a pyriform apparatus borne upon the innermost shell. Adults in mammals and birds, mostly in herbivorous mammals; larval stages unknown. Four subfamilies .....

1. Genital canals dorsal to longitudinal excretory vessels and nerves, except possibly in *Triplotaenia*, and in some proglottids in some *Schizotaenia*. Uterus at the stage of sexual maturity tubular, netlike, or diffuse, or, in *Triplotaenia*,

- saclike. Development usually by outpocketing, the uterus rarely breaking up into separate compartments, never with paruterine organs. Vitelline and shell glands always present. .... *Anoplocephalinae* 2
- Uterus breaks down early into egg capsules. Genital canals pass ventral to excretory ducts or between them. Cortical parenchyma usually very thick. A single set of reproductive organs in each segment in all known species. Vitelline and shell glands always present. .... *Linstowinae* 51
- Paruterine organs present. Genital canals pass between the excretory vessels and dorsal to the nerve. Embryos with two shells, usually with pyriform apparatus which is devoid of horns. Testes in two lateral groups which cross the excretory ducts on either side. Vitelline and shell glands present. .... *Thysanosominae* 70
- Paruterine organs present. Genital canals pass dorsal to excretory ducts or between them. Eggs with two shells, no pyriform apparatus. No vitelline gland or shell gland. All known species inhabit ruminants. (See Gough, 1911.)  
*Avitellininae* 71

## ANOPLOCEPHALINAE

2. Without genital pores. Testes crossing excretory ducts on both sides of the proglottid. No pyriform apparatus. One genus and species. (See Fuhrmann, 1902.) ..... *Aporina alba*
- With genital pores. Testes not crossing excretory ducts on pore side ..... 3
3. With not more than one cirrus pouch in each lateral half of the segment. With numerous testes. With external evidences of segmentation ..... 4
- With four or five cirrus pouches in each lateral half of the segment. With but one testis in each lateral half of the segment. Without external evidences of segmentation. One genus and species. (See von Janicki, 1906.)  
*Triplotaenia mirabilis*
4. With but one set of reproductive organs in each proglottid ..... 5
- With two sets of reproductive organs in each proglottid ..... 6
5. Vaginal pore posterior to cirrus pouch. Uterus reticular. Either with a pedunculated prostate gland or with ventral excretory ducts enormously developed. Genital pores all, or nearly all dextral. (See present paper.) ..... *Andrya* 7

- Vaginal pore posterior, or posterior and dorsal to cirrus pouch. Uterus tubular. No prostate gland. Ventral excretory ducts normal in size. Genital pores alternate, except in the doubtful *Bertiella pinguis* where they are unilateral. Testes anterior. (See Bourquin, 1905.).....*Bertiella* 12
- Vaginal pore and vagina ventral to cirrus pouch. Uterus tubular. No prostate gland. Genital pores dextral except in the doubtful *Anoplocephala omphalodes* and *A. minima*. testes only on the side away from the genital pore, except in *A. spatula* and occasionally in *A. omphalodes*. (See present paper.) .....*Anoplocephala* 21
- Vagina and vaginal pore anterior to the cirrus pouch. Uterus diffuse, degenerate reticular. No prostate gland. Testes either posterior or anterior, and usually mostly on the pore side. (See present paper.).....*Schizotaenia* 30
6. Vagina crosses cirrus pouch ventrally on both sides of the segment. (See Stiles, 1896, and present paper.).....*Cittotaenia* 34
- Vagina crosses cirrus pouch dorsally on the left, and ventrally on the right side. (See Stiles & Hassall, 1893.).....*Moniezia* 44

## GENUS ANDRYA

7. Scolex large. Excretory ducts enormous. No prostate gland. With external vesicula seminalis..... 8
- Scolex and excretory ducts of ordinary dimensions. With prostate gland. Vesicula seminalis confined to cirrus pouch ..... 9
8. Length 10 to 20 cm. Number of proglottids, 350 to 450. Width of strobila, 1.5 mm. Vesicula seminalis very large. Host, *Geomys bursarius*, Minnesota. (See present paper.)  
*A. macrocephala*
- Length 9 to 12 cm. Number of proglottids, 290. Width of strobila,  $\frac{3}{4}$  mm. Vesicula seminalis only two or three times the diameter of the vas deferens. Host, *Geomys bursarius*, Minnesota. (See present paper.).....*A. translucida*
9. European; over 60 cm. long, and 5 to 10 mm. broad..... 10
- North American; 3 to 5 cm. long, not over 2 mm. wide..... 11
10. Prostate gland elongate. Testes comparatively few, mostly on the side away from the pore. Host, *Lepus timidus*, Saxony. (See Stiles, 1896.).....*A. rhopalocephala*
- Prostate gland round. Testes scattered thru entire median field. Hosts, *Lepus cuniculus* and *L. timidus*, Europe. (See Stiles, 1896.) .....*A. cuniculi*

11. Testes transversely elongated. Genital pore near middle of lateral margin. Uterus not extending ventral to ovary. Host, *Evotomys gapperi galei*, of Colorado. (See present paper.) ..... *A. communis*
- Testes not transversely elongated. Genital pores near distal end of lateral margin. Uterus extends ventral to ovary. Host, *Sciurus hudsonica*, Minnesota. (See present paper.) ..... *A. primordialis*

GENUS BERTIELLA (Synonym: Bertia)

12. Genital pores alternate ..... 13
- Genital pores unilateral. Host, *Bucorax abyssinicus*. Not properly described, position not assured. (See Fuhrmann, 1904.) ..... *B. pinguis*
13. Dorsal excretory duct actually dorsal. Three longitudinal nerve trunks on either side. Cirrus pouch very small (except in *B. polyorchis*). Female glands in a dorsoventral row ..... 14
- Dorsal excretory duct dorsomesial to ventral. Cirrus pouch of ordinary size, and well developed (except in *B. rigida*). One longitudinal nerve trunk on either side (no statement for *B. rigida*). Female glands arranged in a transverse row. (always?) ..... 16
- Dorsal excretory duct not known, apparently absent. One nerve trunk. Cirrus pouch of ordinary size, egg-shaped. Female glands in a dorsoventral row. A long, convoluted vas deferens. Host, *Lagidium peruanum*. Not properly described. Assigned by von Linstow (1904) to the genus Bertia, but it is by no means certain that it belongs amongst the Anoplocephalidae ..... *B. forcipata*
- The following poorly known species is placed in the genus Bertia, perhaps correctly so. Strobila 245 mm. or more long by 10 mm. broad. Number of segments about 350. Genital pores very small, irregularly alternate. Dorsal canal lateral to ventral. Cirrus pouch large and elongate. Host, *Simia satyrus*. (See Stiles, 1896; or R. Blanchard, 1891.) ..... *B. satyri*
14. Genital pores regularly alternate. Receptaculum seminis poorly developed. Ovary extends through one-sixth of the field between the excretory ducts and is not bilobed. Host, *Troglodytes niger*, Africa. (See Bourquin, 1905.) ..... *B. studeri*
- Genital pores alternate, frequently with regularity. Ovary extending through about one-fourth the width of the proglot-



- tid, divided into two nearly separated lobes, which are connected by a slender neck. Host, *Cercopithecus callitrichus*. (See Beddard, 1911.).....*B. cercopithecici*
- Genital pores irregularly alternate. Ovary not bilobed..... 15
15. Strobila 14 cm. or more long. Receptaculum seminis globular. Eggs enter uterus in 350th segment. Host, *Mycetes niger*, Paraguay. (See Meyner, 1895, or Stiles, 1896.).....*B. mucronata*
- Strobila 84 mm. long. Receptaculum seminis oval. Eggs enter uterus in 130th segment. Host, *Macacus radiatus*. (See Meyner, 1895, and Stiles, 1896.).....*B. conferta*
- Strobila 51 cm. long. Cirrus pouch of ordinary appearance. Host, *Macacus cynomolgus*, India. (See von Linstow, 1905.) .....*B. polyorchis*
16. More than 21 cm. long. Sexually mature proglottids 26 times as broad as long, ripe proglottids 30 times as broad as long. Cortical layer exceptionally thick, in young proglottids forming five-sixth of total thickness, in older proglottids about three-fourths of thickness. Female glands far from median line. Testes numbering about 110. Host, *Phalangista* sp., New Guinea. Not adequately described. (See von Janicki, 1905.) .....*B. rigida*
- Proglottids not so short. Cortical layer of ordinary thickness..... 17
17. Cirrus spiny ..... 18
- Cirrus not spiny ..... 19
18. Length, 30 to 60 cm. Number of proglottids, 600 to 850. Eggs pass into uterus in 300th proglottid. Testes 70 to 90. Ovary extending past the median line of the proglottid. Host, *Galeopithecus volans*, Sumatra. (See Bourquin, 1905.).....*B. elongata*
- Length, 2 to 6 cm. Number of proglottids, 80 to 200. Genital pores approach regular alternation. Testes 50 to 70. Ovary distant by more than twice its width from the median line. Host, *Galeopithecus volans*, East Indies, Sumatra, Java. (See Bourquin, 1905.) .....*B. plastica*
19. Vitelline gland posterior to the ovary. Length, 14 cm. Number of testes 90, extending to the distal end of the proglottid. Diameter of ovary, 0.95 mm., not greatly displaced from the median line, its mesial edge extending across the median line. Hosts, doves and pigeons. (See Fuhrmann, 1902.) .....*B. delafondi*
- Vitelline gland not posterior to the ovary..... 20

20. Length, 50 to 60 cm. Several thousand proglottids. Testes about 200, reaching the distal limit of the proglottid. Ovary lying one-third beyond the median line of the proglottid. Host, *Phascolarctus cinerus*, Australia. (See Zschokke, 1898.) ..... *B. obesa*
- Length, 66 cm. Number of proglottids, up to 1500. Testes fewer than in *B. sarsinorum*, extending nearly to the posterior limit of the proglottid. Ovary reaching just to the median line of the proglottid. Host, *Phalanger ursinus*, Australia and vicinity. (See Zschokke, 1899.) ..... *B. edulis*
- Length, 7 cm. Number of proglottids, 220. Testes 30 to 40, mostly in a single row at the anterior end of the proglottid. Ovary distant by nearly half its width from the median line of the proglottid. Host, *Phalanger ursinus*, Australia and vicinity. (See Zschokke, 1899.) ..... *B. sarsinorum*

#### GENUS ANOPLOCEPHALA (Syn.: Plagiotænia)

More than half the species placed in this genus are poorly known, and the statements made are often not dependable; some of the species probably do not exist, and others probably belong even in other families. For this reason, a logical key is out of the question, and no attempt has been made to make one; the following arbitrary division is made.

21. At least fairly well known species, generic position assured ..... 22
- Improperly described, position not assured ..... 27
22. Cirrus pouch enormous, 0.8 mm. or more long, lying mostly within the excretory ducts ..... 23
- Cirrus pouch ordinarily not over 0.3 mm. long, more than half of it lying outside the excretory ducts ..... 24
23. Length, 25 to 40 mm. Number of proglottids, 30 to 40. Sexual maturity reached in 10th or 12th proglottid. Receptaculum seminis globular, small. Host, *Tapirus americanus*, Brazil. Not fully known anatomically; all points known are essentially in agreement with the next species. (See Lühe, 1895.) ..... *A. globiceps*
- Length, 10 mm. Number of proglottids, 10 to 28. Sexual maturity reached in eighth or ninth proglottid. Receptaculum seminis large and oblong, mostly ventral to cirrus pouch. Cirrus not spiny. Ovary not bilobed. Hosts, *Lepus cuniculus* and *Lepus variabilis*, France. (See present paper.)  
*A. wimerosa*

- Length, 6 to 30 mm. 35 to 55 proglottids. Cirrus spiny.  
Sexual maturity reached about the 15th proglottid. Host,  
*Equus caballus*, Europe. (See Stiles, 1896; and R. Blanchard,  
1891.) ..... *A. mamillana*
24. Ovary consists of two practically separate lobes. Receptaculum  
seminis greatly elongated. Host, *Equus caballus*, Old  
World. (See Kahane, 1880.) ..... *A. perfoliata*  
Ovary not bilobed ..... 25
25. (The better descriptions are not accessible to me; information  
compiled from several sources). 9 to 80 cm. long. Scolex  
4 to 6 mm. in diameter. Maximum width, 5 to 20 mm.  
Synonyms: *A. plicata*, *A. zebrae*, etc. (See Scheibel, 1895.)  
..... *A. magna*  
Scolex considerably less than 1 mm. broad. Maximum breadth  
not over 5 mm. .... 26
26. Over 3 cm. long. Over 125 proglottids. Host, *Geomys bursa-*  
*rius*, North America. (See present paper.) ..... *A. variabilis*  
Length, 12.5 to 20 mm. Number of proglottids, 60 to 75. Hosts,  
*Geomys bursarius* and *Microtus* sp., North America. (See  
present paper.) ..... *A. infrequens*
27. Genital pores irregularly alternate. Length, 12 to 21 cm. Num-  
ber of proglottids, 250 to 300. Cirrus spiny. Hosts, *Mus*  
*arvalis* and *Mus amphibius*. (See von Janicki, 1906; and  
Stieda, 1862.) ..... *A. omphalodes*  
Genital pores regularly alternate. Length, about 2 mm.;  
breadth, about 0.34 mm. Number of proglottids, 50 to 70.  
Host, pheasant, Italy. Description worthless; nothing to  
indicate that it belongs even in the family, if it exists. (See  
Mello, 1912.) ..... *A. minima*  
Genital pores unilateral ..... 28
28. Testes extending across median field. Length, 25 to 45 mm.  
Number of proglottids, 100. In *Heterohyrax mossambica*.  
Most likely does not belong in this genus. (See Bischoff,  
1912; and von Janicki, 1910.) ..... *A. spatula*  
Testes confined to the side away from the genital pore ..... 29
29. Length, 16 cm. Cirrus spiny. In *Arvicola campestris*. (See  
von Linstow, 1878; and von Janicki, 1906.) ..... *A. inermis*  
Length, 3 to 4 cm. In *Agricola campestris*. (See Moniez, 1891;  
and von Janicki, 1906.) ..... *A. blanchardi*  
Length, about 8 mm. Breadth, 5 mm. Number of proglottids,  
40 to 50. In *Arvicola nivialis*, Italy. Description worth-  
less. Species may not belong to family, if it exists. (See  
Galli-Valerio, 1905.) ..... *A. dentata*

- Length, 10 to 16 cm. Breadth, 6 to 8 mm. 200 to 300 segments. 60 to 80 testes. In *Arctomys* sp., Turkestan. (See Zschokke, 1888; and Stiles, 1896.).....*A. transversaria*  
 No information available. (See Railliet, 1893.).....*A. restricta*

## GENUS SCHIZOTAENIA

30. Genital pores regularly alternate. Testes posterior, except in occasional proglottids in one species. Less than 20 cm. long ..... 31  
 Genital pores irregularly alternate. Testes posterior, extending uniformly across the median field. About 3 cm. long. Hosts, *Dicotyles albirostris* and *D. torquatus*, Brazil. Not well known, position not assured. (See Lühe, 1895.).....*S. decrescens*  
 Genital pores unilateral. Size enormous, up to 120 cm. long, and 7.5 cm. broad. Testes mostly on pore side..... 33  
 31. Testes extending nearly uniformly across the median field in only two or three rows anteroposteriorly. Female glands near the median line so that the ovaries of the two sides overlap for most of their width..... 32  
 Testes nearly all in the half that contains the genital pore. Female glands far from the median line, the ovary not reaching the median line of the proglottid. Hosts, *Erethizon dorsatus* and *E. epixanthus*, North America. (See present paper.) .....*S. variabilis*  
 Testes either extending across the median field, or in two groups separated from each other by the vitelline gland; in either case mostly on the side away from the genital pore, where they are in six or seven rows in the anteroposterior axis. Female glands quite large very near the median line. Host, *Geomys breviceps*, Oklahoma. (See present paper.) .....*S. anoplocephaloides*  
 32. Length, 14 cm. Number of proglottids, about 280. Vitelline gland compact, formed of many small radiating lobes. Walls of vesicula seminalis glandular throughout. Vaginal walls glandular. Host, *Hydrochaerus capybara*, Brazil. (See von Janicki, 1906.).....*S. hagmanni*  
 Length, 3 to 4 cm. Number of proglottids, about 100. Vitelline gland formed of a large median and a smaller lateral lobe. Walls of vesicula seminalis not glandular, except at inner end. Vagina ephemeral, walls not glandular. Hosts,



- Erethizon dorsatus* and *E. epixanthus*, N. America. (See present paper.) ..... *S. americana*
33. Testes relatively few, confined to the anterior portion of the proglottid, mostly on the pore side. Ovary small, pear-shaped. Host, *Rhinoceros sondaicus* (and other rhinoceroses?) (See MacCallum & MacCallum, 1912; *Taenia gigantea*.) ..... *S. gigantea*
- Testes very numerous, filling almost the entire field dorsally. Ovary consists of a transverse portion which extends nearly across the median field, and of numerous clubshaped lobes leading from it. Host, *Rhinoceros indicus* (and other rhinoceroses?) (See Deiner, 1912.) For reasons for transferring to *Schizotaenia*, see present paper..... *S. latissima*

GENUS CITOTAENIA (Syn.: Ctenotaenia)

34. Cirrus pouch pyriform, distinct. Dorsal excretory duct lateral or dorsal of ventral (no statement for *C. bursaria*)..... 35
- Cirrus pouch much elongated and slender, resembling the nozzle of a hose, and less distinct; in old proglottids, sometimes becoming pyriform on account of being gorged with sperm. Dorsal excretory duct generally median..... 39
35. Uterus not a simple transverse tube, but a rather simple reticulum. Length, 40 to 80 cm. Breadth, 15 mm. Number of proglottids, 200 or more. Genital pores in posterior corner of segment. Testes very numerous, scattered thru the dorsal portion of the median field. Host, *Lepus cuniculus*, Europe. (See Stiles, 1896, and others.)..... *C. denticulata*
- Uterus a simple transverse tube..... 36
36. Testes 100 to 150, confined to the region between the two ovaries, not separated into two lateral groups. Host, *Arctomys* sp., France. (See Blanchard, 1891; and Stiles, 1896.)
- C. marmotae*
- Testes extending nearly or quite to the excretory ducts on either side anterior to the ovaries, and not separated into two lateral groups..... 37
- Testes arranged in a group about each ovary, absent from the median part of the field..... 38
37. Length, 55 mm. Each set of genital organs occupies one-fifth the cross diameter of the proglottid. Cirrus pouch short and clubshaped. Testes numerous, spherical,  $44\mu$  in diameter, reaching the posterior end of the proglottid in the

- median part of the field. Host, *Lepus nigricollis*. Locality, Nedunkeni. Inadequately described. (See von Linstow, 1906.) ..... *C. bursaria*
- Length, 180 mm. Testes very numerous, mostly dorsal,  $88\mu$  long by  $53\mu$  broad. Cirrus spiny. Each ovary occupies one-seventh of the cross diameter of the proglottid. Host, *Lagidium peruanum cuvieri*. Locality, Peru. Not well known. (See von Linstow, 1904.) ..... *C. quadrata*
- Length, 40 mm. Number of proglottids, about 150. Dorsal canal lateral. Host, *Geomys bursarius*, Iowa. More thorough description needed. (See Stiles, 1896.) ..... *C. praecocquis*
38. Length, 80 cm. 500 to 750 proglottids. 60 to 80 testes in each group. With pyriform body. Hosts, *Lepus cuniculus* and *Lepus cuniculus domesticus*. Distribution, Europe. Not well known. (See Stiles, 1896.) ..... *C. ctenoides*
- Length, 8 to 9 cm. Number of proglottids, 250 to 350. Testes about 15 or 20 on each side, all dorsal. With pyriform body. (See Zchokke, 1907, under name *Moniezia diaphana*; and present paper.) ..... *C. diaphana*
- Length, 13 to 16 cm. Three longitudinal excretory ducts, true dorsal duct outside. Testes 30 on each side, extending thru medullary portion. No pyriform body. (See von Janicki, 1905.) ..... *C. zschokkei*
39. Diameter of scolex, 1.5 mm. Cirrus pouch  $600\mu$  long and  $20\mu$  in diameter. Testes about 110. Host, *Rhea americana*, of South America. Description very incomplete. (See Fuhrmann, 1904.) ..... *C. rhea*
- With prostate cells on vas deferens ..... 40
- Without prostate cells on vas deferens ..... 41
40. Length, 10 cm. Diameter of scolex,  $230\mu$ . Testes about 200, dorsal. Cirrus pouch  $520\mu$  long and  $20\mu$  wide. Host, *Stringops habroptilus*. Description very incomplete. (See Fuhrmann, 1904.) ..... *C. psittacea*
- Length, 15 to 22 cm. Diameter of scolex,  $800\mu$ . Testes 120 to 140, confined to the region between the ovaries. Cirrus pouch 1 mm. long,  $120\mu$  in diameter. Host, *Anas* sp. (See Fuhrmann, 1897.) ..... *C. avicolae*
41. Dorsal excretory vessel lateral to ventral. Length, 5 cm. Cirrus pouch  $300\mu$  long and  $40\mu$  broad. Hosts, *Carpophaga vanwycki* and *Ptilopus jambu*. Localities, Karavia (New Britain) and Sumatra. (See Fuhrmann, 1902; and Shipley, 1900.) ..... *C. kuvaria*

- Dorsal excretory duct median to ventral..... 42
42. Testes confined to the region between the ovaries. Uterus in anlage crosses excretory ducts dorsally. Excretory system simple. Cirrus pouch 400 $\mu$  long. Hosts, *Sylvilagus floridanus* and *S. palustris*, North America. (See Stiles, 1896; Lyman, 1902; and present paper.).....*C. variabilis*
- Testes extending laterad beyond the ovaries. Uterus in anlage confined to the median field. Fifteen or more large, prominent ducts crossing the proglottid lengthwise and connecting the transverse commissures of the excretory ducts with each other ..... 43
43. Cirrus pouch about 1 mm. long, extending some distance mediad of the longitudinal excretory canals. Testes 100 to 125. Hosts, *Lepus timidus*, *L. variabilis*, and *L. californicus*, Europe and North America. (See Stiles, 1896; Lyman, 1902; present paper, and others.).....*C. pectinata*
- Cirrus pouch not over 640 $\mu$  long, often much shorter. Testes 60 to 80. Hosts, *Sylvilagus floridanus* and *S. pinetis*. (See Hall, 1908, under name *C. mosaica*; and present paper.)  
*C. perplexa*

#### GENUS MONIEZIA (Syn. partim: Paronia)

44. Description not accessible.—*Moniezia beauforti* von Janicki 1906b. Host, *Cyclopsittacus dioptahlmus*, in Sekanto.  
*M. beauforti*
- Length, 20-27 cm. Host, *Macropus giganteus*, Australia. Poorly known, position uncertain. (See R. Blanchard, 1891; or Dujardin, 1845:593.) .....*M. festiva*
- Uterus tubular or slightly branched, not reticular, confined to median field in anlage. In its final stages saccular, or with anterior and posterior outpocketings. Embryos without pyriform apparatus. Dorsal excretory duct dorsal to ventral (not known in *M. variabilis*)..... 45
- Uterus a very complicated, finely meshed reticulum, usually, if not always, crossing the excretory ducts dorsally in anlage. Embryos usually with pyriform apparatus, the horns of which generally end in a disk. Dorsal excretory duct median to ventral ..... 47
45. Uterus in anlage inverted U-shaped, embracing ovary..... 46
- Uterus in anlage a transverse bar, with a few simple branches at its median end. Communication of ripe uteri of two

sides of proglottid slight. Number of testes about 200. With prostate cells on vas deferens. Cirrus pouch  $90\mu$  long. Host, *Ptilopus* sp., Sumatra. (See Fuhrmann, 1902.)

*M. columbae*

46. Uteri of two sides never united. Testes about 140. No prostate cells on vas deferens. Cirrus pouch 300 to  $450\mu$  long. Hosts, *Ptilonopus* sp., *Lorius erythrothorax*, *Trichoglossus novaehollandiae*, *Cyclopsittacus suavissimus*, and other parrots, New Guinea and Sumatra. (See Fuhrmann, 1902; also, Diamare, 1900 and 1901.).....*M. carrinoi*

Uteri of two sides becoming connected very early, anteriorly. Number of testes, about 100. Host, *Chrysotis amazonica*, South America. (See Fuhrmann, 1902.).....*M. ambigua*

- Uteri of two sides becoming connected distally. Hosts, 4 species of Rhamphastos. Description poor. (See Fuhrmann, 1904.).....*M. variabilis*

47. With interproglottidal glands, which are linear, and are not grouped around blind sacs (very indistinct in *M. benedeni*.) *Planissima*-group ..... 48

With interproglottidal glands, which are grouped around blind sacs. *Expansa*-group ..... 49

No interproglottidal glands. *Alba*-group ..... 50

48. Length, 1 to 2 m. Ripe segments 12 to 26 mm. broad, and 1 to 1.75 mm. long. Interproglottidal glands large, distinct. Hosts, *Bos taurus* and *Ovis aries*. (See Stiles & Hassall, and others.) .....*M. planissima*

Length, 4 m. Ripe segments 12 mm. broad by 3 mm. long. Interproglottidal glands indistinct (absent?). Hosts, *Bos taurus* and *Ovis aries*. Better study needed. (See Stiles & Hassall, 1893.) .....*M. benedeni*

About 0.66 m. long. Largest segments 8 mm. broad by 1.5 mm. long. Testes in a quadrangle. Interproglottidal glands small. Host, *Ovis aries*. Better study needed. (See Stiles & Hassall, 1893.).....*M. neumanni*

49. Length, 4 to 5 m. Testes in mature proglottids usually in a quadrangle, rarely in two triangles. Hosts, *Bos taurus* and *Ovis aries*. See Stiles and Hassall, 1893; Tower, 1900; present paper, and others.).....*M. expansa*

Length, about 1 m. Testes less numerous and smaller than in *M. expansa*. Host, *Coassus* sp., Trinidad, South America. Poorly known. (See Stiles and Hassall, 1893.)

*M. oblongiceps*



Length, 1.6 to 2 m. Testes usually in two triangles, absent from median part of the field. Orifices of suckers slitlike. Host, *Ovis aries*. (See Stiles and Hassall, 1893.)

*M. trigonophora*

50. Length, 0.6 to 2.5 m. Testes in a quadrangle. Genital pores in anterior half of the segment. Hosts, *Bos taurus* and *Ovis aries*. Description very incomplete. (See Stiles & Hassall, 1893.) ..... *M. alba*

Length, 41 cm. Testes in entire median field, except part occupied by female glands. No disk figured on pyriform body. Host, *Hippopotamus amphibius*. Description poor, generic position not established. (See von Linstow, 1901.)

*M. amphibia*

Length probably not over 10 cm. Poorly described. Host, *Ateles hypoxanthus*, Brazil. See Lühe, 1895)..... *M. rugosa*

#### LINSTOWINAE

51. Genital pores alternate. Cirrus pouch well developed. Female glands near the median line..... 52  
 Genital pores unilateral. Cirrus pouch weakly developed. Female glands far from the median line, except *Thysanotaenia lemuris* and *Zschokkeella remota*..... 53  
 52. Genital canals ventral to excretory canals and nerve. Cortical layers of great thickness.....Linstowia, 54  
 Genital canals between excretory canals. Cortical layer of ordinary thickness (See Fuhrmann, 1902.).....  
 “*Taenia*” *anoplocephaloides*

53. For the following so-called genera, no differences of generic import are known, with the possible exceptions of *Thysanotaenia lemuris* and *Zschokkeella remota*. It seems most probable that they all belong in the genus *Zschokkeella*, with the two exceptions mentioned. Most of the species are poorly described, so no attempts at rearrangement have been made. They are listed here merely to make the key complete.

Genus <i>Zschokkeella</i> .....	57
Genus <i>Inermicapisfer</i> .....	58
Genus <i>Thysanotaenia</i> .....	68
Genus <i>Hyracotaenia</i> .....	69

## GENUS LINSTOWIA

54. Cirrus pouch very large, reaching to the median line of the proglottid or nearly so..... 55  
 Cirrus pouch relatively small, not reaching to the lateral excretory trunks. Embryos, in ripe proglottids, mostly in lateral portions of the segment..... 56
55. Testes about 40, mostly posterior. Host, *Perameles obesula*, Australia. (See Zschokke, 1898.)..... *L. semoni*  
 Testes about 100, mostly anterior. Host, *Echidna hystrix*, Australia. (See Zschokke, 1898.) Tidswell, 1910, has declared *Taenia echidnae* Thompson 1893 and *Taenia phoptica* Cobbold 1879, to be synonyms. (I have been unable to find this article, or even to learn its title)..... *L. echidnae*
56. Number of proglottids, 160 to 200. Genital pore but slightly in front of the middle of the proglottid. Ovary of about 8 slender lobes, four of which extend towards each lateral margin. Host, *Peramys americana*, South Americana. (See Zschokke, 1904.)..... *L. jheringi*  
 Number of proglottids, 90. Genital pore very near the anterior end of the margin. Ovary consists of two comparatively compact lobes each with very short, slender, radiating processes. Host, *Didelphys tristriata*, Brazil. (See von Janicki, 1906.)..... *L. brasiliensis*
- GENUS ZSCHOKKEELLA (Syn. Zschokkea Fuhrman 1902)
57. Excretory vessels far medial. Testes about 140, largely outside the median field. Host, *Numida ptilorhyncha*... (See Fuhrmann, 1902.)..... *Z. linstowi*  
 Testes in median field. Cirrus pouch round, small, one-eighteenth the diameter of the proglottid. Very poorly described. Most of the facts known point to the conclusion that this cestode does not belong in the genus Zschokkeella; but not enough is known to justify placing it elsewhere. Host, *Oprecopithecus pyrrhonotus*, West Africa. (See von Linstow, 1905.)..... *Z. remota*  
 Excretory ducts lateral in position. Testes in two groups, mostly on the side away from the pore. Host, *Cricetomus gambianum*. (See Beddard, 1911, 1912.)..... *Z. gambianum*

## GENUS INERMICAPSIFER

58. No information of importance. (See von Janicki, 1910.) \_\_\_\_\_  
*I. gondokorensis*  
 Testes filling most of median field..... 59  
 Testes posterior, extending across field..... 60  
 Testes in two lateral groups..... 64
59. 70 to 80 embryo-capsules, with 8 to 10 embryos in each. Number of proglottids, 70 to 80. Length of cirrus pouch, 400 $\mu$ .  
 Host, *Hyrax* sp. (See von Janicki, 1910.).....*I. pagensteckeri*  
 30 to 50 embryo capsules, up to 6 embryos in each. Number of proglottids, 40. Length of cirrus pouch, 270 $\mu$ . Host, *Hyrax* sp. Locality, Schoa. (See Bischoff, 1912.).....*I. paronae*
60. Number of embryo capsules, 100 or more. Number of proglottids, 300 or more..... 61  
 Number of embryo capsules, 75 or less. Number of proglottids 130 or less..... 62
61. (No valid point of distinction from next. Length, 111 mm. Number of proglottids, 300. Host, *Hyrax capensis*. (See von Janicki, 1910.).....*I. critica*  
 Length, up to 350 mm. Number of proglottids, 400 to 500. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.)  
*I. hyracis*
62. Number of embryo capsules, 75; 5 to 7 embryos in each. Number of proglottids, 130. Number of testes, 80. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.).....  
*I. interpositus*  
 Number of embryo capsules, 24 to 28. Less than 60 testes..... 63
63. Length, 40 mm. 8 to 10 embryos in each capsule. 50 to 60 testes. Host, *Hyrax*, sp., Erethrea. (See Bischoff, 1912.).....  
*I. abyssinicus*  
 Length, 15 to 20 mm. 5 embryos in each capsules. 40 testes. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.).....  
*I. prionodes*
64. Number of proglottids, 200. Host, *Procavia capensis*. (See Beddard, 1912.).....*I. capensis*  
 Number of proglottids, not over 70..... 65
65. 5 to 7 embryos in each capsule..... 66  
 10 to 15 embryos in each capsule..... 67
66. Cirrus pouch 130  $\mu$  long. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.).....*I. parvulus*

- Cirrus pouch 270  $\mu$  long. Host, *Hyrax* sp., East Africa. (See Bischoff, 1912.).....*I. apospasmation*
67. 20 to 70 proglottids. Host, *Procavia* sp., South Africa. (See von Janicki, 1910.).....*I. settii*
- 12 to 15 proglottids. Host, *Hyrax* sp., Rikwasee. (See Bischoff, 1912.).....*I. lopus*

## GENUS THYSANOTAENIA

68. Female glands near the median line of the proglottid. No dorsal excretory duct. Host, *Lemur macaco*. (See Beddard, 1911b, 1912.).....*T. lemuris*

## GENUS HYRACOTAENIA

69. Ovary entirely, or partly laterad of ventral excretory duct. Vitelline gland dorsal. Host, *Procavia capensis*. (See Beddard, 1912.).....*H. procaviae*
- Ovary entirely mediad of excretory ducts. Vitelline gland ventral. Host, *Procavia capensis*. (See Beddard, 1912.).....*H. hyracis*

## THYSANOSOMINAE

## GENUS THYSANOSOMA

70. Length, 15 to 30 cm. Two sets of reproductive organs. Testes in median field. Posterior flap of segments fimbriate. With pyriform body, which has no horns. Reported from several species of *Cervus*, *Cariacus*, *Bos* & *Ovis*. (See Stiles & Hassall, 1893.).....*T. actinioides*
- Length, 1 to 2 m. Seldom more than one set of reproductive organs to the proglottid, pores alternating irregularly. Testes in lateral fields. Posterior flap of segments fimbriate. With pyriform apparatus which has no horns. Hosts, *Ovis*, *Bos*, and *Sus*. (See Stiles & Hassall, 1893.).....*T. giardi*
- Length, 1.5 m. Strobilization not distinct. Genital pores alternating rather regularly. No pyriform apparatus. Host, *Capreolus pygærdus*, Siberia. Description unsatisfactory. (See Kholodskovi, 1902.).....*T. pygardi*

## AVITELLININAE

71. Uterus single; a single paruterine organ. Testes in four groups. Genital canals pass dorsally of both excretory ducts.....*Avitellina* 72
- Uterus double; two paruterine organs. Testes in two groups. Genital canals pass between excretory canals.....*Stilesia* 73



## GENUS AVITELLINA

72. Length, 2 or 3 meters. Host, *Ovis aries*, Africa, Italy. (See Gough, 1911.).....*A. centripunctata*

## GENUS STILESIA

73. Testes mostly median or dorsal to the ventral canal. Hosts, ruminants, Africa. (See Gough, 1911.).....*S. hepatica*  
 Testes all lateral to the ventral canal..... 74
74. Vas deferens forms a dense packet of convolutions (functionally a vesicula seminalis) between nerve and ventral canal before reaching cirrus pouch. Host, *Camelus dromedarius*, India and Algiers. (See Gough, 1911.).....*S. vittata*  
 Vas deferens forms at most 3 or 4 loose convolutions between the nerve and ventral canal, before reaching the cirrus pouch. Hosts, *Ovis* & *Capra*, Europe and India. (See Gough, 1911.).....*S. globipuncta*

## SUMMARY AND CONCLUSIONS

1. The cestodes of the subfamily Anoplocephalinae are in some way dependant upon rich soils for their existence and they thrive best in wet lowlands. The evidence points to the conclusion that the intermediate hosts are some group of insects which is confined to such regions; and since the hosts of the Anoplocephalidae are almost exclusively herbivorous, it would seem as if this host were a small, plant-feeding insect.

2. The primitive Anoplocephaline uterus was of the reticulate type, which in turn was derived from a median longitudinal tubular uterus by lateral outgrowths. The transverse tubular and diffuse uteri of this group have been derived from the reticular by simplification.

3. In the early primitive Anoplocephalidae the uterus crossed the excretory ducts ventrally; subsequently it became restricted to the median field and later came to cross the excretory ducts dorsally.

4. The position of the vaginal pore and vagina is one of the most stable anatomical characters of the Anoplocephalinae and should be given recognition as one of the most important criteria of relationship. The primitive position of the vagina was posterior to the cirrus pouch.

5. The more generalized representatives of the genus *Andrya* approach the nearest of all known Anoplocephalidae to the ancestral types of the family. Leaving out of consideration the aberrant *Triplotaenia*,

the genera *Moniezia* and *Schizotaenia* constitute the highest types of the Anoplocephalinae; the other subfamilies of the family seem to have sprung from forms like these two genera.

6. Cestodes exhibit a high range of variability which should be taken strictly into account in morphological, phylogenetic, and systematic studies. Generalizations not founded upon plenty of material and careful study and reflection do more harm than good. The following reference list of variations and anomalies reported in this paper shows the need of extreme caution in coming to conclusions regarding structure and consequent relationships.

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## EXPLANATION OF PLATES

Unless otherwise stated all drawings were drawn to scale, measurements being made with an ocular micrometer, and are dorsal side uppermost, with the anterior end towards the top of the plate.

## ABBREVIATIONS USED

<i>C</i>	genital cloaca	<i>RS</i>	receptaculum seminis
<i>CP</i>	cirrus pouch	<i>SG</i>	shell gland
<i>ExD</i>	dorsal excretory vessel	<i>T</i>	testis
<i>ExV</i>	ventral excretory vessel	<i>UD</i>	uterine duct
<i>ExT</i>	excretory tubes connecting transverse commissures.	<i>Ut</i>	uterus
<i>N</i>	longitudinal nerve trunk	<i>Va</i>	vagina
<i>O</i>	ovary	<i>VC</i>	ventral transverse commissure
<i>Ovd</i>	oviduct	<i>VD</i>	vas deferents (Plates V and VI)
<i>Par</i>	parenchyma-filled spaces between the compartments of the uterus	<i>VD</i>	vitelline duct (Plates I and III)
<i>PG</i>	prostate gland	<i>VD<sub>ef</sub></i>	vas deferens (Plate I)
		<i>VE</i>	vasa efferentia
		<i>VG</i>	vitalline gland
		<i>VS</i>	vesicula seminalis

## EXPLANATION OF PLATE

Figures 1 to 4. *Andrya primordialis*.

Fig. 1. Proglottid at sexual maturity, dorsal view; ovary and uterus omitted.

Fig. 2. Proglottid at sexual maturity, ventral view, to show ovary and uterus.

Fig. 3. Uterus of nearly ripe proglottid.

Fig. 4. Scolex, drawn from temporary mount.

Figures 5 to 8. *Andrya communis*.

Fig. 5. Proglottid at sexual maturity, dorsal view; ovary and uterus omitted.

Fig. 6. Proglottid at sexual maturity, ventral view, to show ovary and uterus.

Fig. 7. Ventral view of vitelline and shell glands and female genital ducts.

Fig. 8. Diagram of excretory ducts and cirrus pouch, showing a different arrangement from that shown in Figure 5.

Figures 9 to 11. *Andrya macrocephala* (see also next plate).

Fig. 9. Mature proglottid, dorsal view, uterus omitted.

Fig. 10. Mature proglottid, ventral view, to show uterus.

Fig. 11. Fully developed uterine embryo, middle membrane omitted.



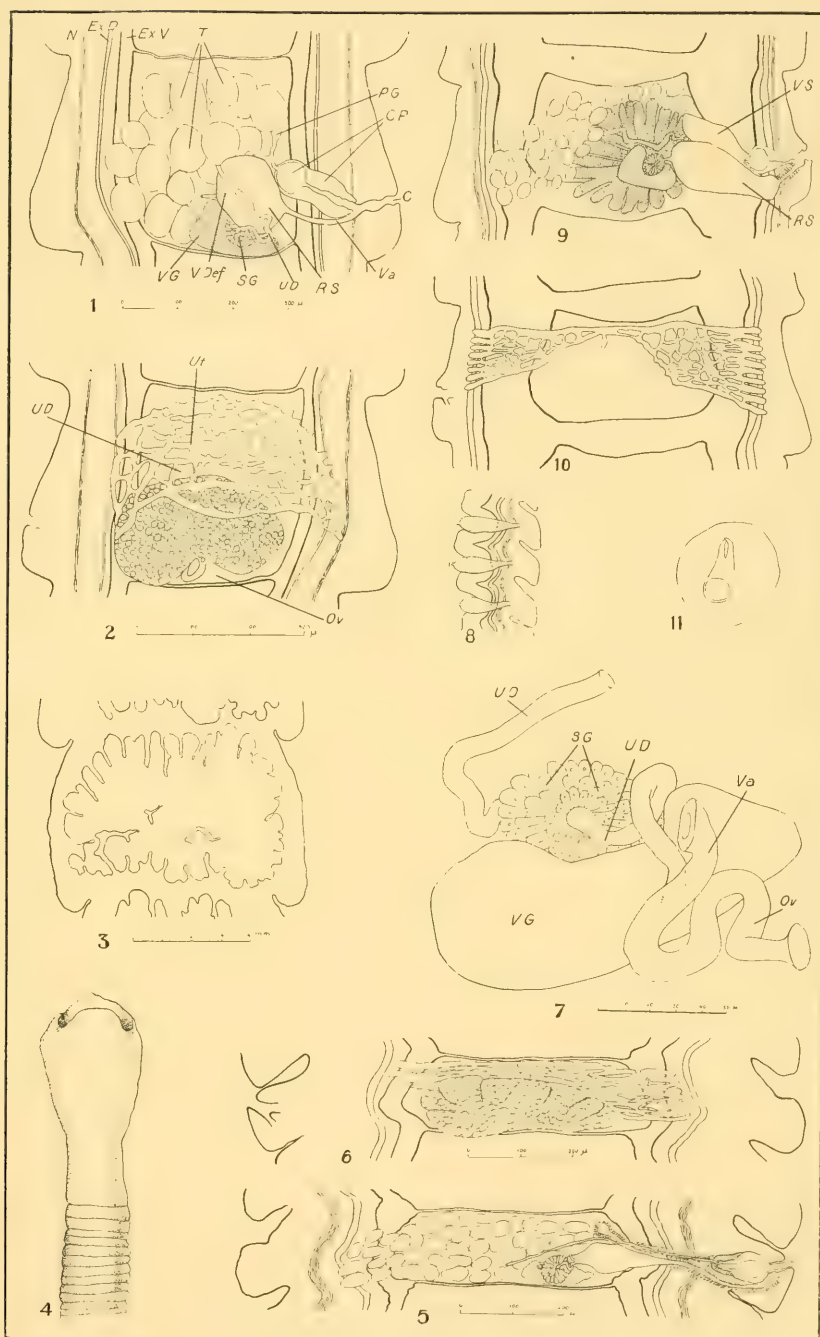


PLATE I



## PLATE II

## EXPLANATION OF PLATE

Figures 12 and 13. *Andrya macrocephala* (see also Plate I).

Fig. 12. Uterus of ripe proglottid.

Fig. 13. Section of scolex.

Figures 14 to 16. *Andrya translucida*.

Fig. 14. Mature proglottid, dorsal view.

Fig. 15. Mature proglottid, dorsal view; ovary and shell gland omitted.

Fig. 16. Mature proglottid, ventral view, showing ovary and uterus.

Fig. 17. *Anoplocephala wimerosa*. Mature proglottid, dorsal view.

Figures 18 to 21. *Anoplocephala variabilis* (see also Plate III).

Fig. 18. Section of scolex in expanded condition.

Fig. 19. Section of scolex in contracted condition.

Fig. 20. Uterus of ripe proglottid.

Fig. 21. Uterine embryo, middle membrane not represented.



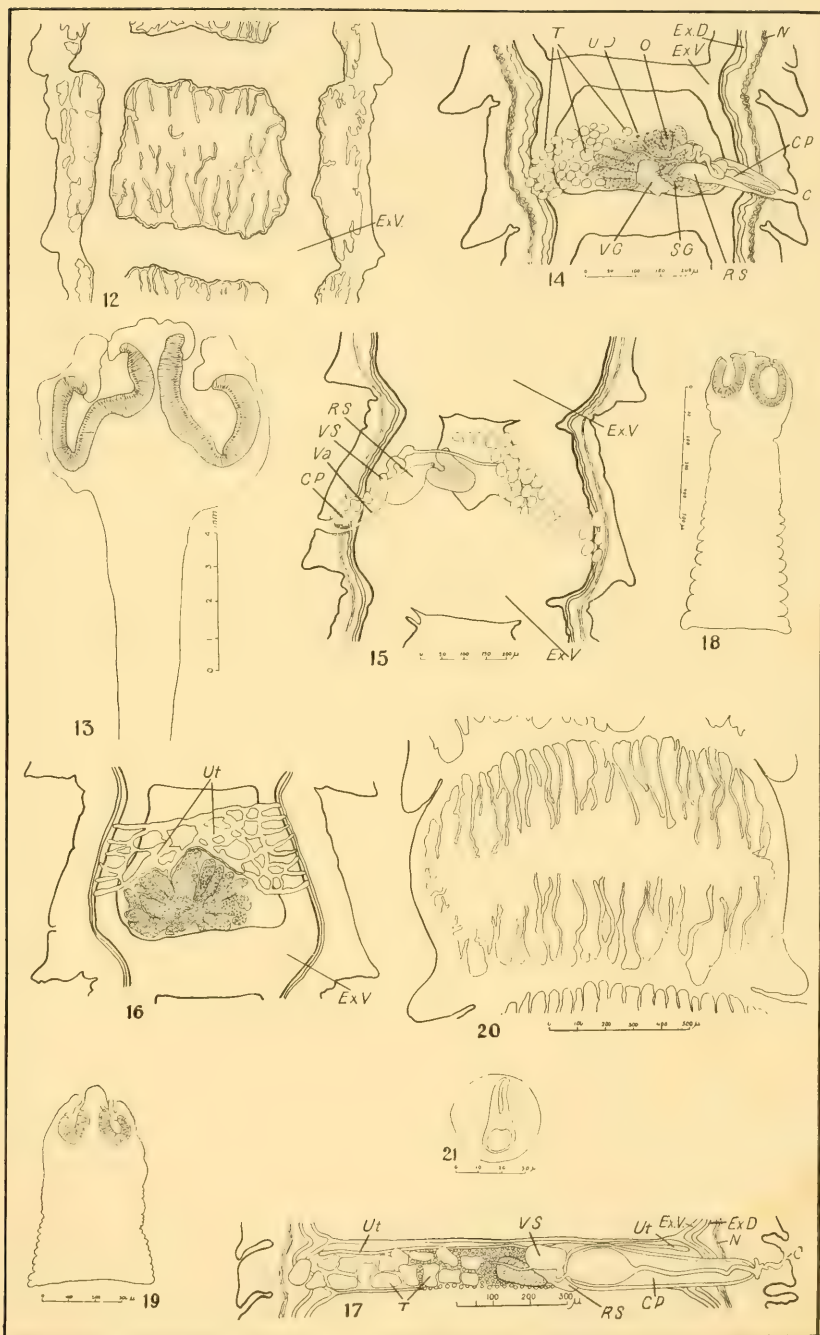


PLATE II



**PLATE III**

## EXPLANATION OF PLATE

Figures 22 to 24. *Anoplocephala variabilis* (see also Plate II).

Fig. 22. Mature proglottids in contracted condition; some structures omitted.

Fig. 23. Mature proglottid in expanded condition.

Fig. 24. Vitelline gland, shell gland, and female ducts; expanded condition, ventral view.

Figures 25 to 27. *Anoplocephala infrequens*.

Fig. 25. Mature proglottids in ventral view, some structures omitted. The transverse commissures of the ventral ducts which appear straight here are sinuous in dorsoventral plane.

Fig. 26. Section through the scolex.

Fig. 27. Vitelline gland, shell gland, and female ducts; ventral view.



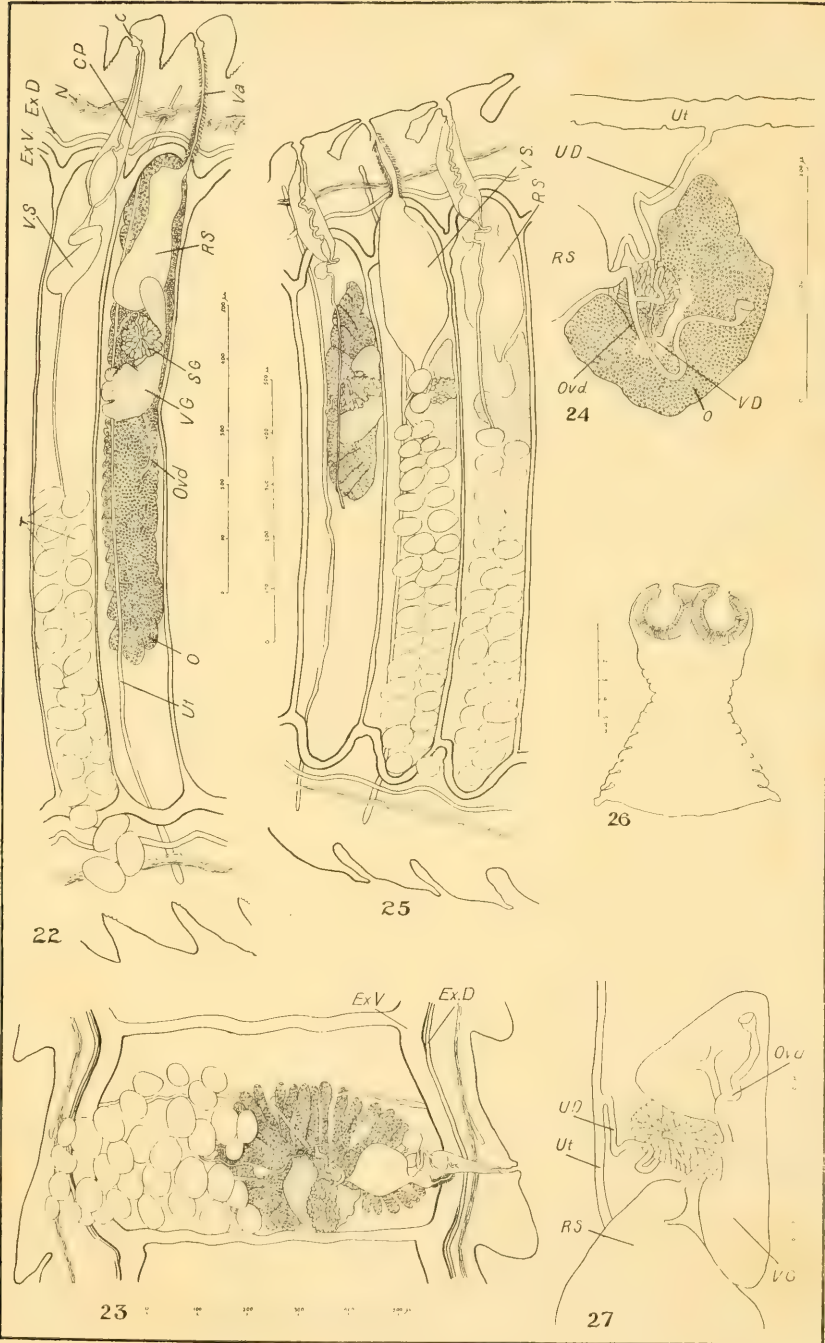


PLATE III



## PLATE IV

## EXPLANATION OF PLATE

Figures 28 and 29. *Schizotaenia americana*.

Fig. 28. Mature proglottid, dorsal view; uterus not included.

Fig. 29. Mature proglottid, showing uterus (dotted), oviduct, and shell gland.

Figures 30 to 32. *Schizotaenia variabilis*.

Fig. 30. Mature proglottid, dorsal view. After this drawing was completed the study of additional material showed that it is not normal in some respects, namely: (1) the testes are usually further forward, anterior to the transverse commissure; (2) the accessory ventral commissures were found in only one specimen; (3) the vesicula seminalis is usually not thrown into wide curves as here shown. The uterus may be somewhat more extensive than here shown; the poor condition of the material does not permit exact judgment as to the limits of this structure.

Fig. 31. Diagram of excretory system of five adjacent proglottids, showing accessory transverse commissures (*AVC*) and other features. The absence of the main transverse commissure in some cases may be due to the fact that the proglottids are not fully mature.

Fig. 32. Drawing showing the cloaca only partly everted and the cirrus pouch lying consequently mostly mediad of the excretory ducts.



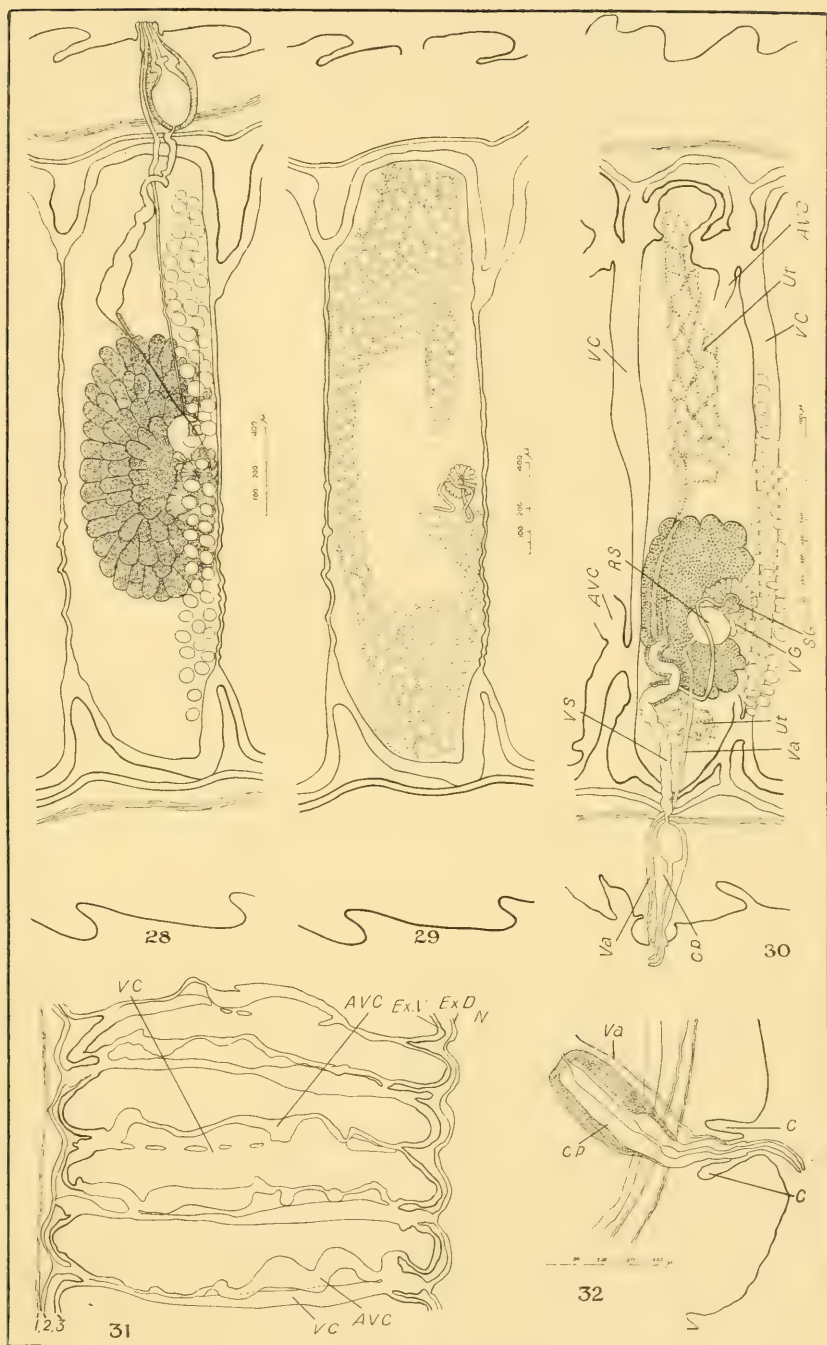


PLATE IV



## PLATE V

## EXPLANATION OF PLATE

Figures 33 to 40. *Schizotaenia anoplocephaloides*.

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Fig. 37. Section of scolex thru suckers.

Fig. 38. Scolex and anterior regions from toto mount.

Fig. 39. Fully developed uterine embryo, middle embryonic membrane omitted.

Fig. 40. Diagram to show excretory system in a series of proglottids. Drawn ventral side uppermost.



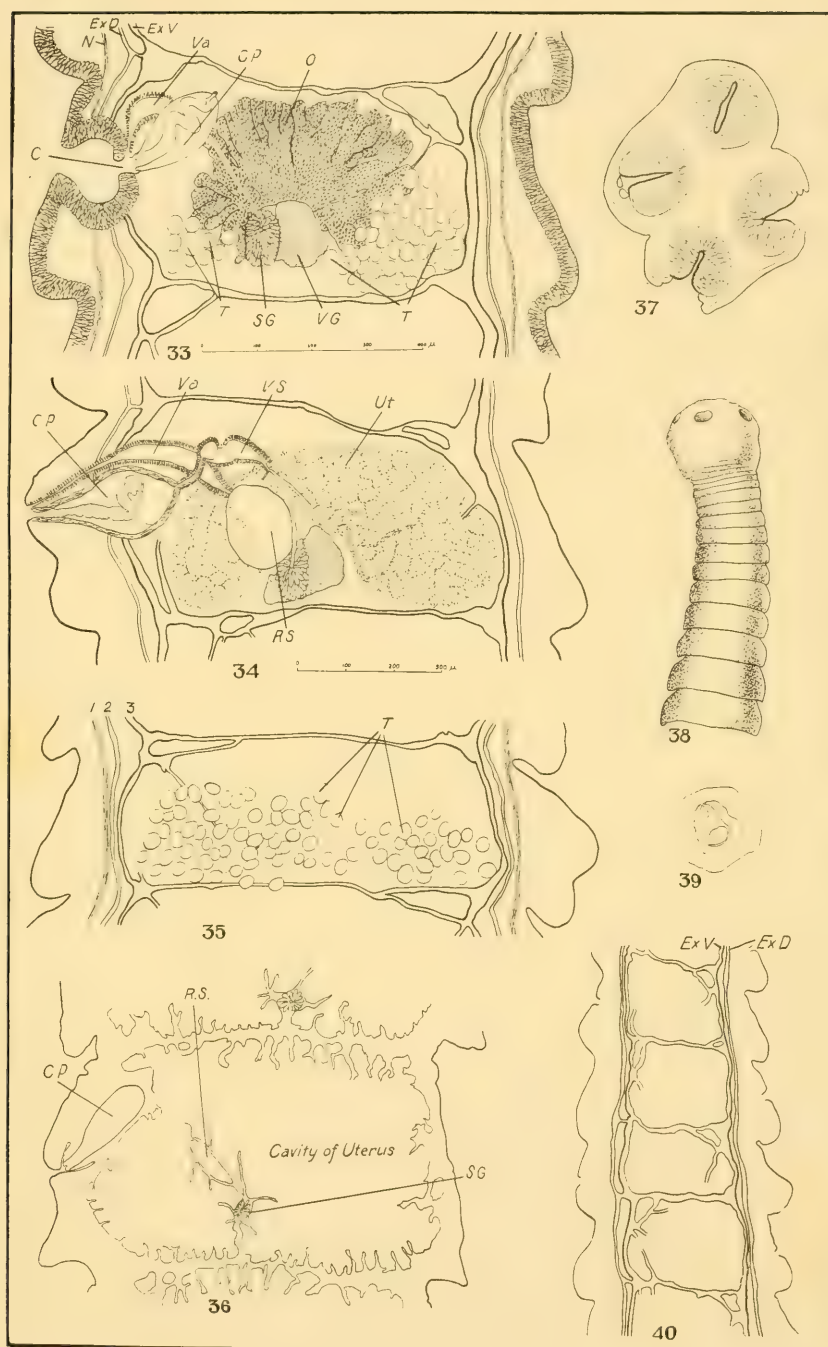


PLATE V



## PLATE VI

## EXPLANATION OF PLATE

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Fig. 42. Uterus as it appears just prior to the entrance of the eggs, a complicated network of interconnecting small tubes.

Fig. 43. Uterus in its final stages, a system of separated or nearly separated compartments.

Figure 44. *Cittotaenia variabilis*. Proglottid at sexual maturity, dorsal view; parts of genital ducts and female glands omitted from left side.

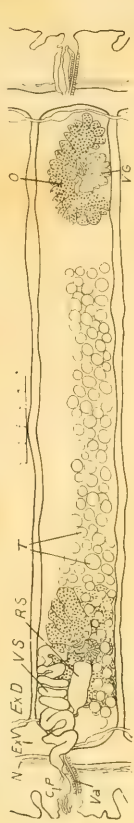
Figure 45. *Cittotaenia pectinata americana*. Proglottid at sexual maturity, dorsal view.

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Figures 47 to 49. Cirrus pouches, showing variations in size and form. All drawn to the same scale.

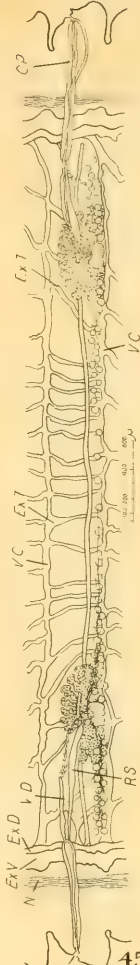




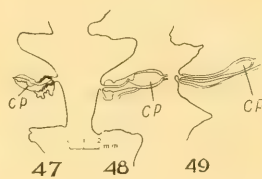
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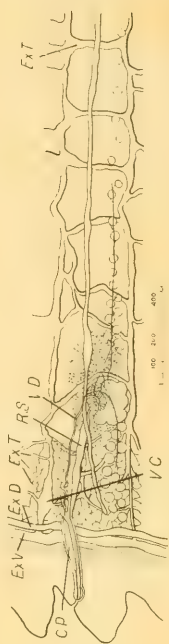
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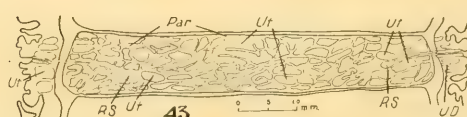
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SOME NORTH AMERICAN  
LARVAL TREMATODES

WITH EIGHT PLATES

BY

WILLIAM WALTER CORT

Contributions from the  
Zoological Laboratory of the University of Illinois under the direction of  
Henry B. Ward, No. 44

THESIS

Submitted in Partial Fulfilment of the Requirements  
for the Degree of Doctor of Philosophy  
in Zoology in the Graduate School  
of the University of Illinois  
1914

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## INTRODUCTION

Practically nothing is known of the life-histories of the trematodes of North America. Even in Europe where many new adults are being described each year only a few developmental cycles are completely known. One reason for this is to be found in the difficulties involved.

Two methods of attacking trematode life-history problems have been employed. One is to attempt to prove specific identity between cercariae and adults by structural comparisons, and the other is to attempt to find the relationship experimentally. Positive results from the first method have been few. The structure of certain types of cercariae gives no suggestion of the family to which the adult belongs, and in the more differentiated forms generic identification is very rarely possible. Even when the comparison is narrowed to very similar cercariae and adults from limited localities it is safest to consider the results as merely suggestive. Many errors have crept into the literature from too much reliance on this method. In some cases the mere suggestion of probable identity by one author has been taken by another as if it were an established fact. It is only when the adult has been experimentally raised from the cercariae or the larvae from the eggs of the adult that the establishment of specific identity can be made sure. The experimental method of study also has its dangers. The factors involved are so complex and so little understood that only the most carefully controlled experiments can be considered as conclusive. In some very recent work as well as in older papers larvae and adults, shown later to be entirely unrelated, have been joined experimentally.

In connection with efforts to solve developmental problems it is often argued that given the structure of a cercaria, it is possible to draw conclusions as to the environment where it encysts, the life it leads, etc. Further, that if the course of development of one member of a group is known, it can be concluded that the others follow the same lines. Dollfus (1914) finds evidence against both generalizations. He states that after a comparative examination of cercariae and the environment in which they live, he can assert that cercariae very similar in structure dwell in different hosts and have very different kinds of development, and that cercariae very different morphologically live

in identical environments and have similar courses of development. Certainly in the study of the development of digenetic trematodes it will be necessary to increase very greatly the number of particular instances known before the induction of general principles can safely go very far.

In Europe, where more is known of trematode development than elsewhere, the foundations of this study were laid in the middle of the last century by the work of such men as Leuckart, Wagener, Pagenstecher, La Valette St. George, de Filippi, and Moulinié. Altho they made but little progress in the actual working out of developmental cycles, their descriptions of large numbers of cercariae from molluscs have formed the basis for later work. In England Nicoll and Marie Lebour have very recently made some headway in the study of larval trematodes altho as yet little experimental work has been done. In North America only a beginning has been made in the study of adult trematodes and as yet there are only a very few scattered observations of larval stages. The present work was undertaken by the writer at the suggestion of Professor Henry B. Ward as an attempt to open up this almost untouched field in North America.

Most of the descriptions of larval trematodes from North American molluscs are very inadequate and in many cases it is impossible to tell to which general group of cercariae the forms belong. In only a very few instances are either drawings or measurements given. The following list is an attempt to bring together all references to date on larval trematodes from North American molluscs.

1. *Cercaria hyalocauda* Haldeman (date?) also reported by Evarts (1880). Host *Physa heterostropha* Say. Locality (?).
2. *Cercaria bilineata* Haldeman (1840). Host *Limnea catascopium*, Camden, Delaware.
3. *Cercariaeum vagens* (Leidy) (1847: 220-221)  
     Syn. *Distoma helcis* (Leidy 1847:220-221)  
         “ *pericardium* Creplin (1849)  
         “ *vagens* Leidy (1850: 304-310)  
     *Cercariaeum helcis alternatae* Diesing (1855:398)  
         398)  
         “ *vagens* Diesing (1858:42)  
     Host *Helix alternata* and *Helix albolabris*, Philadelphia, Pa.
4. *Cercaria agilis* Leidy (1858: 110). Found free in the Delaware river.
5. *Monostoma (Glenocercaria) lucania* Leidy (1877:200-201)  
     Host *Planorbis parvus*. Philadelphia, Pa.

6. *Distoma (Gymnocephala) ascoidea* Leidy (1877:201). Host, *Planorbis parvus*, Philadelphia, Pa.
7. *Distoma centrappendiculatum* Leidy (1890:416).  
Syn., *Distoma appendiculatum* Leidy (1877:202).  
Host, *Helix arborea*, Philadelphia, Pa.
8. *Distoma cornifrons* Leidy (1878:382-383). Host, *Donax fosser*, Cape May, New Jersey.
9. *Distoma lasium* Leidy (1890). Host, *Ilyanassa obsoleta*, Beach Haven, New Jersey.
10. *Cercaria platyura* Leidy (1890:415-416). Free in a pool at Fort Bridger, Wyoming.
11. Cercaria of *Diplodiscus temporatus* Stafford, Cary (1909). Host, *Goniobasis virginica*, Princeton, New Jersey.

The present paper adds fourteen new species of cercariae from North American fresh-water snails. A preliminary report, taking up briefly the structure and activity of these cercariae has already been published (Cort, 1914).

#### METHODS OF STUDY

To obtain this material examinations were made of large numbers of snails from various localities. I want to express my thanks to Dr. Ruth Marshall, Dr. M. F. Guyer, Dr. G. R. La Rue, Dr. B. M. Allen, Dr. F. W. Carpenter, Dr. H. S. Pratt, Mr. A. F. Coutant, Mr. Hermann Douthitt, Dr. C. S. Mead, Dr. A. Richards, Dr. C. C. Nutting, and Dr. J. E. Ackert for their kindness in collecting and shipping me living snails. Without their aid it would have been impossible to have obtained the material for this study.

To Professor Henry B. Ward, under whose direction this work has been carried on, I wish to express my appreciation for his interest and helpful suggestions.

The following method was employed in the examination of snails for larval trematodes. The shell was cut or crushed so as to remove the body, if possible, unbroken. An examination was then made with the low power of the microscope. If larval trematodes were present, some of them were almost invariably loosened from the infected part and scattered around the snail in the water. The digestive gland was the organ most usually infected, its color being often changed by the pigmentation of the sporocysts or rediae. When infection was found a part of the diseased tissue was preserved whole for sectioning, an-

other portion was teased apart to free the larvae for preserving for toto mounts, and the remainder was used for the study of the living animals. Much of the anatomy of the cercariae could be made out from living specimens. In fact this proved to be an extremely important part of the study, since some points, for example the smaller branches of the excretory system and the movement, could only be observed in this manner.

For preservation of material a number of fixatives were used. In fixing the freed cercariae for toto mounts the best results were obtained by the use of hot solutions of Bouin's picro-aceto-formol or corrosive-acetic. For sectioning the infected organs were fixed in toto, since as suggested by Cary (1909:597) this is easier and gives better results than attempting to section freed individuals. A corrosive-acetic solution was ordinarily used for fixing this material. Rediae and cercariae for toto mounts were stained in Mayer's haemalum, Delafield's haematoxylin, Conklin's picro-haematoxylin, and Mayer's paracarmine. The specimens were as a rule considerably overstained in dilute solutions of the stain and differentiated in  $\text{HCl}_2$  under the microscope. In mounting it was found convenient to place large numbers of the larvae on one slide. The infected organs to be sectioned were usually stained in bulk in Ehrlich's acid haematoxylin, cut into sections 5 to 7 micra in thickness, and differentiated on the slide, part of them being counterstained in eosin.

On account of their great mobility, small size, and remarkable power of changing their shapes, some cercariae are very difficult objects to study. No very accurate measurements can be made of living specimens, and in preserved material they are often contracted and distorted. With the living cercariae an attempt was made to get the range of variability, and in preserved material, whenever possible, the average measurements of a number of well extended specimens were taken. The measurements of preserved material are less than those from living specimens of the same kind, even the suckers shrinking perceptibly after preservation. For these reasons comparisons of the cercariae based on size and shape, as Lühe (1909:173) has suggested, are not always by themselves very reliable criteria for specific determination.



## MONOSTOME CERCARIAE

About five per cent., of the largest specimens of *Physa gyrina* from a drainage ditch north of Urbana, Illinois, examined in December, 1913, were infected with the rediae and cercariae of a monostome. I propose to name this species *Cercaria urbanensis*. The infection was in the liver of the snail and there were present both rediae in different stages of development and free cercariae. No sporocysts were found and none of the rediae contained rediae. It is interesting to note that in the descriptions of monostome larvae no mention is made of sporocysts, and only one observation of rediae developing from rediae. Braun (1892:805-806) notes that in certain of the monostomes rediae are already developing in the free swimming miracidia, which he considers to already represent sporocysts. Looss (1896:197) states that in material of *Cercaria imbricata* Looss collected from *Bythinia tentaculata* near Leipzig, rediae were present in which rediae were developing. From this he concludes that the life-history of this species is accomplished in the same manner as that of the amphistomes, which have several generations of rediae.

When freed from the liver of the snail the redia had considerable power of extension and contraction. The immature ones especially stretched out the anterior end and reached in all directions. No locomotor appendages were present either in young or mature redia and no locomotion was noted. In fact the redia of *Cercaria imbricata* Looss is the only monostome redia that is reported with locomotor appendages. According to Looss (1896:196) the appendages in this species were well marked in the young redia but more or less effaced with advancing age. In some of the largest rediae of *Cercaria urbanensis* very peculiar annular constrictions were noted in different parts of the body, which divided it into two or three separate regions connected by very narrow passages (Fig. 12). These constrictions seem to be due to temporary unequal contraction states in different regions of the circular body muscles. This condition for the redia of *Cercaria urbanensis* was observed only in preserved material. Leidy (1877:200; 1904:143-144) notes such constrictions in the living redia of a monostome cercaria which he calls *Monostoma lucanica*.

The methods of locomotion of *Cercaria urbanensis*, either when swimming in open water or when upon a substratum, are very striking. The body when swimming was contracted almost into a round ball and the tail, which was curled ventrally so that it passed across the ventral surface of the body, lashed backward and forward with great rapidity. This method of locomotion was very effective and the cercariae could be seen even with the naked eye in rapid movement thru the water. In spite of the lack of a ventral sucker the cercaria was able to move well on a surface by utilizing two projections which form the posterior lateral angles of the body. In the process of locomotion the cercaria took hold with its oral sucker and the body contracted until it was practically round. Then the sucker let go its hold and the body stretched out, at the same time extending the posterior projections until they became little points digging into the substratum. Again the oral sucker took hold and again the body contracted. By a continued repetition of these movements this cercaria progressed at about the same rate of speed as those having two suckers. After each contraction the posterior projections held the amount gained. During the contraction and at the beginning of the extension of the body the tail kept lashing very rapidly, but during the rest of the movement it was held still and somewhat contracted.

Some of the freed cercariae after moving around for a while settled down and formed cysts. A cercaria which was moving along on a surface extended and contracted its body more and more slowly, until while retaining a hold with the oral sucker the body became almost round. While in this position the cystogenous material was extruded, and the appearance was soon given of a round cyst with a tail attached. Soon the worm inside freed itself from its connection with the tail and squirmed around in the cyst. Finally the tail wriggled loose from the cyst and continued swimming around for considerable time, resembling in form and movement a free living nematode. The cysts formed in a watch glass were flattened on the lower surface and had much the shape of a chocolate drop. The process of encystment is illustrated by figures 1, 2, 3, and 4. Encystment in the open has been noted for *Cercaria ephemera* Nitzsch. The encystment of this species, which was first reported by Nitzsch (1807), was the first described for a cercaria. La Valette St. George (1855:33-34) described and figured the process for the same species, and in one of his figures shows the tail attached to the cyst. Von Linstow (1896:377) for *Cercaria monistomi* von Linstow describes the encystment in the same host as the larval generation.

The rediae of *Cercaria urbanensis* (Figs. 10, 11, and 14) were in various stages of development, varying in length from 0.52 mm. to 1.08 mm. and in width from 0.12 mm. to 0.22 mm. In shape they are elongate sac-like forms smallest at the anterior and widest a short distance in front of the posterior extremity. The mouth is at the anterior tip and the pharynx varies with the size of the animal. In the smallest redia studied which had a length of 0.52 mm. the pharynx was 0.038 mm. in length by 0.048 mm. in width while in one 1.08 mm. in length it was 0.07 mm. by 0.08 mm. The passage thru the pharynx immediately opens into the intestine which is at first narrow but soon widens greatly. In all stages of development the intestine is proportionally very large, having a diameter of from one-third to two-thirds the width of the body and reaching to within 0.08 mm. to 0.16 mm. of the posterior end. It is rather clear and transparent and contains only a small amount of food material floating in a considerable quantity of fluid. The outer cuticula of the redia is very thin and can hardly be distinguished as a separate layer. Inside of this is a very strong layer of circular muscles which encircle the body as separate strands, each about 0.0018 mm. in width and about the same distance apart. The strands of the longitudinal layer are very thin and only visible under favorable conditions. Inside of the muscle layers are several rows of parenchymatous cells with rather large nuclei. These cells do not form a circumscribed lining of the body cavity but are irregular and in young rediae where the lining is several cells thick, strands extend from them thruout the body cavity forming an irregular network (Fig. 13). Into this loosely filled space between the body wall and the intestine the cercariae push. In the oldest rediae the wall has been reduced to one layer and the movements of the cercariae have broken down the parenchymatous strands and converted the region between the wall and the intestine into a well defined cavity, which is more or less completely filled with developing cercariae. In the posterior end of the redia is the germ gland, in front of this are germ balls and further forward in the older rediae are differentiated cercariae. In the youngest redia (Fig. 10) studied the developing embryos were all back of the middle of the body and the furthest developed was a mass of embryonic cells about 0.09 mm. in length and 0.06 in width and having no tail. In none of the rediae was the body cavity crowded with cercariae, there being but two or three well developed forms, and in one mature specimen there were no differentiated cercariae present leaving the body cavity empty for about two-thirds of its length. These conditions and the fact that the oldest cercariae in the rediae are not fully mature and that matured and almost matured cercariae are found



free in the livers of the infected snails, show that the cercariae as they develop are continually making their way out of the rediae to finish their growth in the liver of their host. The most highly differentiated cercaria found in the redia (Fig. 11, 14, cr) was 0.3. mm. in length and 0.1 mm. in width and had a tail 0.22 mm. in length. The two lateral eye-spots were developed and the pigment was present to a considerable extent around them, but was not further scattered or concentrated to form the so-called intermediate eye-spot. Outlines of the longitudinal vessels of the excretory system and the anlage of the reproductive system could be clearly distinguished. The oral sucker was well defined but none of the rest of the digestive system could be distinguished.

The mature *Cercaria urbanensis* (Fig. 5) varies greatly in shape being at greatest contraction nearly round, about 0.27 mm. in length and 0.20 mm. in width and when extended 0.54 mm. long and 0.11 mm. wide. When not in motion the tail is contracted being about 0.2 mm. long and 0.05 mm. wide at its base. At times of greatest movement the tail becomes attenuated to about one-half its usual diameter and often reaches a length of 1.2 mm. It is weakly attached to the dorsal mid-line of the posterior end of the body and tapers to a sharp point. There is an inverse ratio between the contraction of the body and the tail for when the body is most contracted the tail is most extended and vice versa.

In view of the great power of movement of *Cercaria urbanensis* the histological structure of its tail is of considerable interest. Just inside of the thin cuticula is a layer of circular muscles arranged as strands separated by about twice their length from each other. Inside of this is a very strong layer of longitudinal muscle fibers each 0.0026 mm. in diameter. Next comes a single layer of parenchymatous cells somewhat irregularly elongated with nuclei 0.005 mm. in diameter. Extending the length of the tail and forming a core are two rows of long cells which are close together and have their long axes parallel with the length of the tail. These cells vary in size having a length from 0.028 mm. to 0.035 mm. In a cross section of a tail 0.075 mm. wide one of these cells measured 0.026 mm. in thickness and 0.014 mm. in width. They are full of heavily staining granules and their nuclei are 0.007 mm. in diameter. There is nothing suggestive of a possible function for these cells. Figure 9, a cross section thru a tail, shows the structures described above.

At the posterior lateral angles of the body are projections which may be extended to aid the animal in locomotion. The tips of these projections are made firm by structures which appear to be infoldings



of the outer cuticula. One of the structures (Fig. 8) is ovoid with two cuticular walls, having a loosely fitted space between them, and a very narrow central cavity communicating with the exterior by a small pore at the tip of the projection. They apparently have no sucking action, since no muscles are present and the central cavity contracts when the projection is extended. They evidently have a function in locomotion analogous to setae. Similar locomotor projections have been described for *Cercaria ephemera* Nitzsch and *Cercaria imbricata* Looss, and for Leidy's (1877:200) (1904:143-144) *Monostoma lucania* from North America they are merely mentioned as conical projections. Ssinitzin (1905, Plate 4, figs. 75 and 76) figures these structures in *Cercaria ephemera* Nitzsch as clearly circumscribed projections with a considerable cavity lined with spines. Figures 6a and b are copies of his figures. Certainly the structures figured by Ssinitzin differ considerably from those of *Cercaria urbanensis*. Marie Lebour (1907:442) in the monostome cercaria from *Paludetrina stagnalis* which she considers to be *Cercaria ephemera* describes the posterior locomotor projections as sucker like structures, which are circular in outline and divided in two by a bar. Her figure shows them as structures quite comparable to those of *Cercaria urbanensis* but very different from Ssinitzin's figures. She assigns no especial reason for considering them to be sucking structures. The posterior locomotor projections as described by Looss (1896:194) for *Cercaria imbricata* offer still greater differences. The cavity is comparatively large with but one cuticular wall and divided at its center into two parts by a projection. Figure 7 is a copy of Looss', Plate 14, Figure 151.

Mature specimens of *Cercaria urbanensis* are heavily pigmented especially at the anterior end, and have two lateral pigmented eyes with lenses and a central anterior spot which is formed by a condensation of pigment. The eyes are situated dorsad at each side of the large esophageal commissure and above the obtuse angles formed by the large nerves which pass forward and backward. Each true eye is formed by a mass of pigment in the form of a cup the bottom of which is thicker than the sides. A lens fits into the opening of the cup, leaving a space between its lower surface and the bottom of the cup. An eye spot has a diameter 0.017 mm. and the depth of the pigment cup is 0.024 mm. At the anterior end surrounding each eye are scattered pigment granules extending in all directions and about as clearly defined ventrally as dorsally. Anteriorly a condensation forms the so-called anterior eye spot, and scattered granules reach well beyond the limit of the oral sucker. Posteriorly the pigment granules become more

scattered and continue as two longitudinal lines to the posterior end of the body on each side of the excretory bladder (Fig. 5, p. 1). These lines of pigment extend thru the whole dorsal ventral thickness of the body and are as apparent on one side as on the other. Along each edge and appearing ventrally are two other irregular lines of pigment which do not extend as far back. Little pigment flecks are scattered from these lines out thru the body. In the young cercaria the pigment develops first around the eyespots in dense masses and spreads gradually with growth both forward and backward along the lines mentioned. It is only in the oldest cercaria that it is spread sufficiently to form the anterior spot and the lines extending to the posterior end.

The digestive system (Fig. 5) of *Cercaria urbanensis* is like that described for other monostome cercariae. The mouth at the anterior tip is sub-ventral and the oral cavity is surrounded by a relatively small oral sucker, averaging 0.043 mm. in length and 0.049 mm. in width. The esophagus is very narrow and 0.05 mm. to 0.06 mm. long depending on the contraction. The cecal bifurcations are close together at their beginnings but soon spread further apart. They are always within and slightly dorsad of the large longitudinal excretory vessels and extend almost to the end of the body. The ceca are not yet functional, being composed of a solid mass of cells.

The excretory system (Fig. 5, ex) is typical of the group. At the posterior end is the excretory bladder opening just below the base of the tail. From this extends forward two large vessels which unite in the midline just back of the oral sucker. Thruout their whole course they are filled with small round concretions which disappear in the process of preservation. It is very difficult to be positive of the relations of the excretory system of the tail but as nearly as they can be made out they are as follows: No openings could be found in the tail and a single vessel passed forward from near the tip becoming larger nearer the body and opening at the excretory pore.

Almost the whole body of *Cercaria urbanensis* is filled when mature with large unicellular cystogenous glands containing small granules. Only the very anterior tip, the posterior locomotor projections and the tail are free from them.

Only a few monostome cercariae have been recognized. All of these except *Cercaria lophocera* Filippi (1857:5) correspond very closely in structure to *Cercaria urbanensis*. *Cercaria imbricata* Looss is distinguished by the fact that the rediae have smaller intestines and lateral appendages and by the structure of the posterior locomotor projections of the cercaria (Looss 1896:192-197). Several different forms have

probably been described as *Cercaria ephemera* as it seems improbable that Ssinitzin and Lebour have described the same form. The only difference that can be definitely determined by comparing the descriptions of *Cercaria ephemera* with *Cercaria urbanensis* is in the structure of the posterior locomotor appendages of the cercaria. In von Linstow's (1896:376-377) description of *Cercaria monostomi* both rediae and cercariae are larger than in any of the other species, the arrangement of pigment is different from that in *Cercaria urbanensis*, and no posterior locomotor appendages are described. These may have been overlooked as they are very small and not easily seen unless the animal is studied alive. *Cercaria lophocera* described by Filippi (1857:5) from Italy is entirely different from all other monostomes known.

Two descriptions of monostome cercariae have been made from North America. Leidy (1877:200-201) describes as *Monostoma lucanica*, a form from *Planorbis parvus*. Unfortunately not enough detail is given to make the comparison possible. The other form is described by Haldeman as *Cercaria hyalocauda*. It has been impossible to find Haldeman's original description. Evarts (1880) describes this species from *Physa heterostropha*. Altho so little detail is given that a minute comparison cannot be made between this species and *Cercaria urbanensis*, certain points can be definitely made out. *Cercaria hyalocauda* is about half again as large as *Cercaria urbanensis*, and its cyst is much larger than that of the latter species, being 0.32 mm. to 0.20 mm. It seems evident that the two forms are not identical.

Altho monostome cercariae have been known since 1817, the life-history of no one of them has been proven experimentally. Looss (1896:-192-193) argues from distribution and structural correspondence that *Cercaria imbricata* from Egypt is the larval form of *Notocotyle triseriale* from the duck. Lühe (1909:178) suggests that *Cercaria ephemera* is the larval form of either *Notocotyle triseriale* or *Catantropis verrucosa* (Frol.), but cannot belong to *Typhlocoelum flavum* (Mehl.) on account of differences in the digestive systems of the two forms. So little is known of the monostomes of the United States that it is useless to generalize in regard to the life-history of *Cercaria urbanensis*.

#### AMPHISTOME CERCARIAE

Amphistome cercariae of two species were collected from specimens of *Planorbis trivolvis* from three localities. Two snails out of eighteen from Lawrence, Kansas had the livers infected with rediae and very large pigmented cercariae. Out of large numbers of *Planorbis trivolvis* examined from around Urbana, Illinois, one from a small pond



was infected with this same form. The second of these species, a smaller unpigmented cercaria, was found in one of twenty specimens of *Planorbis trivolvis* from a small pond in the suburbs of Chicago. In all the infected snails mature and immature cercariae were found free in the liver, the mature forms being nearest the periphery, and the active rediae contained no fully developed cercariae. There were no sporocysts present and no rediae in which rediae were developing, and in none of the infected snails were rediae or cercariae numerous. Since the large pigmented species is very unwieldy in movement, I propose to name it *Cercaria inhabilis*, and the smaller species on account of the way in which it changes its body shape will be given the name, *Cercaria diastrophæ*.

*Cercaria inhabilis* swam sluggishly in open water. It contracted its body and lashed its tail backward and forward, moving in an unwieldy, irregular fashion. In fact the body was too large in proportion to the size of the tail for rapid locomotion. On a substratum the cercaria extended and contracted the body but was unable to move by the aid of its suckers.

When in a state of average contraction, about that of figure 16, the body of *Cercaria inhabilis* is pear shaped, tapering in the anterior half, and wider but of uniform diameter posteriorly. It is the largest of the cercariae studied, having an average length in mounted specimens of 0.8 mm. and a width of 0.4 mm. The thickness is a little greater than half the width. The oral sucker is elongate, 0.16 mm. in length and 0.12 mm. in width with the retrodorsal pharyngeal pockets which are characteristic of some amphistomes. The acetabulum is very large averaging 0.23 mm. in diameter; it is at the posterior end of the body and is turned ventrad.

Two large eye-spots are present just back of the pharynx. They are located from one-fourth to one-third of the distance from the anterior to the posterior end, and in a specimen 0.27 mm. wide at this region, they were 0.065 mm. from the outer margins and 0.13 mm. apart. These eyes are composed of the lens and the cone of pigment like those already described for the monostome, *Cercaria urbanensis*. Figure 17, a section thru the eyes, shows them in their relation to the nervous system and other adjacent structures.

In the development of *Cercaria inhabilis* the pigment starts in the eyes and is deposited first in a peculiar way over most of the anterior half of the body. In the youngest cercariae found outside of the rediae very little pigment is seen and that found near the eyes (Fig. 18, p.). In forms a little older (Fig. 19, p.), the pigment has



begun to spread out a little forward and to the sides, but for the most part backward along two irregular lines. At first all the pigment strands were connected in an irregular way, but soon at the ends of the lines little flecks were scattered out. Backward along the lines the pigment becomes thicker (Fig. 20, p) and collects at points of union in the network masses. At an older stage, (Fig. 21, p) the pigment strands from the two lateral lines become connected and form an irregular network about the middle of the oral sucker, laterad as far as the sides, and backward to about the middle of the body. As the cercariae become older the masses and lines of pigment break up and are more scattered. In the mature specimen (Fig. 16) the pigmentation shows as scattered brownish flecks extending thru the whole thickness of the body (Fig. 17, p) and reaching from the oral sucker back to the middle.

The cystogenous glands in *Cercaria inhabilis* are as thickly developed dorsally as ventrally, and extend from the oral sucker to the acetabulum. Viewed from the surface they appear as small rounded bodies, 0.012 to 0.016 mm. in diameter, filled with rod-shaped cystogenous granules. Figure 17 shows them to be elongate, unicellular, club-shaped glands with small nuclei.

The tail of *Cercaria inhabilis* varies from one-third to greater than the body length. It is attached to the tip of the body above the acetabulum and is easily lost in free swimming animals. The cuticula of the tail is very thin and no trace could be found of circular muscles. The longitudinal muscle layer, however, is conspicuous and is formed of a series of strands each 0.0035 mm. in thickness, which extend from the base to the tip. Inside of the muscles is a layer of irregular parenchymatous cells, with nuclei 0.005 to 0.007 mm. in diameter, and irregular indistinct cell boundaries. The space between this layer and the excretory tubule, which courses down the center of the tail, is filled with large cells with faintly granular cytoplasm, and large nuclei, 0.008 to 0.009 mm. in diameter. These cells are similar to those forming the core of the tail of *Cercaria urbanensis*, but inclose no such darkly staining granules. Several of these cells may occur in one cross section since they do not seem to be arranged in regular rows. The central excretory tubule of the tail has a considerable diameter, and contains in its walls very large scattered nuclei, 0.01 to 0.012 mm. in diameter. A cross section of the tail (Fig. 22) shows these structures.

A comparison of the nucleoli of the different nuclei of the tail of *Cercaria inhabilis* is interesting. Of the three kinds of nuclei present viz. 1. nuclei of the excretory tubule, 2. nuclei of the large central cells, 3. parenchymatous nuclei, the first two have large very clearly defined nucleoli and little if any chromatin scattered outside of it. Of

these two the second is the larger. In the parenchymatous nuclei the nucleoli are quite small, not definite in outline, and much chromatin is scattered thru the nucleus.

The excretory vessel in the tail of *Cercaria inhabilis* is a large single tube running down almost to the tip, where it divides to open to each side (Fig. 16). This vessel becomes narrow as it passes from the tail to the body but immediately widens into the excretory bladder, which is a triangular vesicle dorsal and anterior to the acetabulum. No vessels or flame cells were made out in the acetabulum. Into each corner of the bladder open vessels which were traced only as far as the eye-spots. In these vessels were present the round highly refractive concretions, already noted in the excretory system of *Cercaria urbanensis* and by Looss in the amphistome cercariae described by him (Looss, 1896:181).

The mouth of *Cercaria inhabilis* is at the anterior tip of the oral sucker which juts out slightly from the body. The anterior margin of the mouth cavity is smooth or only slightly roughened. There are no papillae present around the margin of the oral cavity such as Looss (1896:179) describes for the amphistome cercaria from Egypt, which he considers, to be the larva of *Gastrodiscus egyptiacus*. The mouth opens into an oral cavity, from which a narrow passage runs directly backward; this changes into the esophagus at the posterior limit of the oral sucker. Into each side of the oral cavity open the blind tubes of the retrodorsal pharyngeal pockets (Fig. 16, pp.). The oral cavity has a length of 0.059 mm. and the lateral blind tubes are 0.086 mm. in length. As it passes out of the oral sucker the digestive tube becomes the thin, straight-walled esophagus, 0.021 mm. in caliber, which has a length of 0.1 to 0.15 mm. depending on the state of contraction of the cercaria. Just before the esophagus bifurcates it is reinforced by a mass of circular muscle fibers of a sphincter, making a characteristic structure which superficially resembles a pharynx. This pseudo-pharynx is about as long as wide, being 0.038 mm. in diameter, and has a wall 0.009 mm. thick, composed of from 12 to 14 separate layers of muscles. Longitudinal muscles were not made out either in this region or in the esophagus. The inner lining of the esophagus is non-cellular and tiny projections extend out into its lumen (Fig. 17, es). After bifurcation the intestinal ceca run laterally for a short distance and then turn posterior to reach within 0.05 mm. to 0.06 mm. of the anterior margin of the acetabulum. The ceca are fairly wide, 0.028 mm. to 0.036 mm., and the inner walls contain flattened nuclei which jut out a little into their lumina. Figure 16 illustrates the relations of the digestive system.

In *Cercaria inhabilis* the anlage of the reproductive organs begins to take definite shape. It is composed of dense masses of small heavily staining nuclei. In the largest cercariae four areas connected by lines are marked out. At the middle line of the body just back of the bifurcation of the intestinal ceca, is an elongate mass which reaches up very close to the ventral surface. This is probably the anlage of the ends of the ducts of the reproductive system, leading up to the genital pore. Slightly back of this and close together are two masses, the primordia of the testes, and further back is the largest densest mass which represents the ovary and its surrounding structures (Fig. 16, ra).

Along with the cercariae in the livers of the infected snails were numbers of active rediae all in about the same stage of development (Fig. 15). When they were freed from the snail they were very mobile extending and contracting and making some progress even on the smooth surface of the watch glass. There were two pairs of locomotor appendages and the posterior extremity was attenuated and pointed. The anterior pair of locomotor appendages was just back of the posterior limit of the intestine and at normal extension the second pair was about the same distance back. The tail region was shorter and more slender. These proportions varied greatly with the contraction of the animal. In alcoholic material the locomotor appendages of the redia are often obliterated by the contraction of the muscles.

One of the largest of these rediae (Fig. 15) measures 1.36 mm. in length and 0.31 mm. in width, and the posterior limit of the voluminous intestine is 0.56 mm. from the anterior tip. The pharynx is very small in proportion to the size of the body, measuring 0.086 mm. in length and 0.065 mm. in width. The intestine contains dark brown material evidently from the liver of the host. Bunched around the anterior tip of the redia just back of the oral sucker are elongate unicellular glands of the type often found in rediae, which send forward ducts to open near the tip.

The cuticula and muscle layers of the rediae of *Cercaria inhabilis* are quite thin. The circular muscles are the strongest but do not show externally. Inside of the muscles except in the region of the anterior part of the intestine and the germ gland, the wall is made up of a layer of cells which is thin in the older forms. In none of the rediae are embryos much differentiated, the largest showing mere stumps of tails, the beginning of suckers and traces of eye-spots. Since immature cercariae are found outside of the redia it is evident that they make their way out at a very early stage, and complete their development free in the snail's liver.



Since *Cercaria diastrophæ* resembles *Cercaria inhabilis* closely the description will be limited to pointing out the differences. As in *Cercaria inhabilis* different stages of development of the cercaria are found free in the snail. The mature cercariae extended and contracted their bodies very actively but none were noted swimming freely. This may have been due to the condition of the material studied. There was no check on the one examination.

*Cercaria diastrophæ* (Fig. 23) is cylindrical in cross section, pointed anteriorly, and when not contracted or flattened the region in front of the acetabulum is but little wider than that sucker. In living specimens the body varied from 0.27 to 0.54 mm. in length according to the state of contraction, and the width changed from 0.20 to 0.08 mm. The tail is always shorter than the body, being 0.22 mm. to 0.38 mm. in length and with an average width near its base of 0.054 mm. The tail is attached dorsad to the acetabulum, which is terminal and forms a flattened base for the conical body (Fig. 24). The oral sucker is elongate and in a specimen of average contraction has a length as great or greater than the acetabulum. In an animal about the state of contraction of Figure 23 the oral sucker had a length of 0.11 mm. and a width of 0.065 mm. and the acetabulum had a diameter of 0.105 mm.

The eye-spots are like those already described but are larger in proportion to the size of the body than in *Cercaria inhabilis*. Except for a very limited area around the eyes *Cercaria diastrophæ* is entirely unpigmented.

The body is filled with cystogenous glands from the oral sucker to the acetabulum.

On account of the freedom from pigmentation it was possible to work out the excretory system further in *Cercaria diastrophæ* than in *Cercaria inhabilis*. Figure 23, ex, shows the relations of this system. The tail vessel and the bladder are alike in both forms. The much convoluted crura of *Cercaria diastrophæ* which are large and contain scattered concretions, extend as unbranched vessels up to the region of the eyes. There they receive small branches from all parts of the body. It was possible to trace the largest of these branches altho on account of the cystogenous glands, the flame cells and the smallest ducts were not found. Into the tips of the crura open on each side two vessels, one from the side of the oral sucker and one from the posterior end. The posterior branch is soon divided into an outer and an inner vessel, which subdivide to reach all parts of the posterior body region.



The digestive system in *Cercaria diastrophæ* is similar to that of *Cercaria inhabilis*, but the oral sucker and its pouches are larger in proportion to the size of the acetabulum, and the intestinal ceca reach nearer the posterior end of the body.

In *Cercaria diastrophæ* the anlage of the reproductive organs is further developed than in *Cercaria inhabilis*. It is differentiated into four clearly separated areas, which bear the same general relation to the adult organs as in the other species. They are not however connected with strands of nuclei and are not in exactly the same relative position as in *Cercaria inhabilis*.

The above descriptions show that *Cercaria inhabilis* and *Cercaria diastrophæ* differ considerably in the size and shape of the body, the ratio in size of the suckers and in the position of the acetabulum, the amount of pigmentation, and in the anlage of the reproductive organs.

Rediæ of *Cercaria diastrophæ* (Fig. 25) were in different stages of development. No rediæ were found in which other rediæ were developing and in none were the cercariæ further developed than in the rediæ of *Cercaria inhabilis*. The rediæ were very mobile, having remarkable power of changing their shape, and with the aid of the posterior locomotor appendages could move fairly well. In the younger rediæ the body would sometimes be extended to five or six times the length when contracted. This mobility is correlated with the extreme development of the circular muscles, which show clearly as annular bands (Fig. 25, ab). In the young living redia part of the excretory system could be made out. One longitudinal trunk from the anterior extremity was traced until it met two trunks from the posterior end.

In the youngest redia studied there were practically no germ balls in the body cavity; the length of a toto mount slightly contracted was 0.45 mm. and the greatest width 0.13 mm. The intestine extended to a point 0.22 mm. from the anterior end and was relatively voluminous. The oral sucker had a length of 0.43 mm. and a width of 0.032 mm. One of the largest specimens measured 0.78 mm. in length and 0.16 mm. in width. The intestine reached one-third the body length. The oral sucker was about the same size as in the younger specimens, the length being 0.044 mm. and the width 0.038 mm. From the above description it is evident that the redia of *Cercaria diastrophæ* is very much like that of *Cercaria inhabilis*. The greatest difference is in a greater mobility correlated with a greater development of the circular muscles in the former.

Altho a large number of adult trematodes belonging to the family Paramphistomidae has been described, I have found in the literature

mention of only three cercariae belonging to this group. The cercaria of *Diplodiscus subclavatus* has been known for a long time, having been first described by de Filippi and best described by Looss (1892:162-166). Of the two other forms one was first described by Sonsino (1892) as *Cercaria pigmentata*, and later shown experimentally by Looss (1896:185-191) to be the larval form of *Amphistomum conicum* (*Paramphistomum cervi*). The other was also described by Looss (1896:177-185) as the larva of *Gastrodiscus aegyptiacus*. This conclusion, however, only rests on the structural comparison of the cercaria and the adult.

The five amphistome cercariae now known belong to two different sub-families of the *Paramphistomidae*. The cercaria of *Paraphistomum cervi* differs from the others in lacking the pockets of the oral sucker, and in having a connection between the longitudinal crura of the excretory system. It belongs to the sub-family *Paramphistominae*. The other four of these cercariae are much alike and belong to the sub-family *Diplodiscinae*. They all have the retrodorsal pockets of the oral sucker, and the muscular enlargement of the esophagus at the bifurcation of the intestinal ceca. *Cercaria diastrophia* differs considerably from the other three in its small size, lack of pigmentation and in the proportionally large size of the oral sucker. The cercaria of *Diplodiscus subclavatus*, that of *Gastrodiscus aegyptiacus* and *Cercaria inhabilis* are very similar. The first of these differs from the other two in the large size of the pharynx of its redia and in the small size of the intestine. *Cercaria inhabilis* is larger than Looss' cercaria of *Gastrodiscus aegyptiacus*. My measurements show that the oral sucker of this species is twice as large as his, and the acetabulum is very much larger. There is nothing in *Cercaria inhabilis* to correspond to the papillae found by Looss around the mouth of his form, and the intestine of the redia is much larger in his species.

The only adult trematode which I have found in the literature from the United States which resembles these cercariae in structure is *Diplodiscus temporatus* Stafford. This form has the retrodorsal pharyngeal pockets found in the cercariae and also the muscular thickening of the esophagus. The arrangement of the reproductive organs is such that those of the adult might be derived from the anlage of either of the above cercariae. As far as conclusions from comparative structure are concerned either *Cercaria inhabilis* or *Cercaria diastrophia* might be the larvae of *Diplodiscus temporatus*. Infection experiments alone can clear up this point. It is evident, that Cary (1909) is mistaken in the larval form which he assigns to *Diplodiscus temporatus*.

Cary (1909) described as belonging to the life-history of *Diplodiscus temporatus* Stafford sporocysts and rediae, both containing cercariae

from *Goniobasis virginica* obtained near Princeton, New Jersey. In 1911 Cary sent me some of the material which he had used in the preparation of this paper, including specimens of *Diplodiscus temporatus* from his experimental tadpoles. A study of this material and a careful analysis of Cary's account has convinced me that he has described in this paper, two different species of larval trematodes neither of which belong to *Diplodiscus temporatus*.

The snails of the species *Goniobasis virginica* which he collected from the Delaware and Raritan canal near Princeton in the fall of 1908, contained rediae in which cercariae were developing, but those collected from the same locality in the spring of the following year and those from the Delaware river near Trenton, contained sporocysts in which cercariae were developing. Cary assigns both these stages unhesitatingly to the same species, for no other reason so far as can be judged than that they were collected from the same species of snail from the same general locality. That in the same species of trematode, cercariae should be found developing from both sporocysts and rediae is without parallel. Further in his own descriptions Cary shows that he is dealing with two separate types of larvae. In connection with his account of the development of the cercariae in the sporocysts, (p. 643), he writes of the cercaria.

"In the dorsal part of the sucker (oral sucker) there is developed the dart (Stachel). This lies in a thin structureless sheath between the muscle cells. It is shaped like a short arrow with a comparatively broad head."

Neither in the description nor in the figure (Cary, 1909, Pl. 30, Fig. 6) of the cercaria which develops from a redia is a dart shown. Further a comparison of the cercariae developing from rediae with the others developing from sporocysts from the material which Cary sent me, shows that they are entirely different in practically every character. Figures 26 and 27 are drawings made to scale of these two types of cercariae. According to Lühe's (1909) classification of the cercariae these forms would fall into two entirely unrelated groups. The smaller one with the boring spine which develops in the sporocysts (Fig. 26) very evidently belongs in the Xiphidiocercariae (Lühe, 1909:189-200) while the larger form agrees with the characteristics of the Gymnocephalous cercariae (Lühe, 1909:182-186). That two such diverse cercariae should develop into the same adult is utterly impossible. Since in his infection experiments Cary uses only the cercariae which develops from rediae, he certainly can have no evidence that the cercariae which develops from sporocysts and are entirely different from the first type have any connection whatever with *Diplodiscus temporatus*.



Therefore Cary's whole discussion in the embrological part of the paper (pp. 617-647) which is based on the study of the sporocysts and the cercariae developing in them cannot without further evidence be given a place in the life-history of *Diplodiscus temporatus*. Since it proves the thesis that Cary sets out to make that the embryo in the sporocysts develops from parthenogenic eggs, this account is a very important contribution to trematode embrology.

Another point in Cary's paper which is very striking is the great difference between the cercaria which he describes as belonging to *Diplodiscus temporatus* and other amphistome cercariae, especially that of *Diplodiscus subclavatus*, of which Looss has worked out the life-history (Looss, 1892). A comparison of these two forms shows striking differences in the shape and size of the body, in the size and position of the acetabulum, in the excretory system especially that of the tail, and in their activities and encystment. (Compare Cary, 1909, Pl. 30, Fig. 6 and Looss, 1892, Pl. 20, Fig. 20). That cercariae belonging to the same genus should be so different in structure is contrary to all the accepted views of trematode development. The few observations found in the literature on the life-histories of closely related species of trematodes show a closer structural correspondence between the cercariae than the adults.

A study of Cary's material shows that he is in error in the description and drawing of the largest of the two cercariae in certain fundamental points. In his drawing (plate 30, Fig. 6) and description the digestive system of the cercaria corresponds to that of the adult *Diplodiscus temporatus*, in having pharyngeal pouches and in the muscular enlargement of the esophagus at the point of division into the intestinal ceca. In his material the cercaria has no pharyngeal pouches and the clearly circumscribed pharynx which is followed by an enlarged portion of the esophagus is entirely different from his description and drawing for this form. Compare figure 27 and Plate 30, Figure 6 of Cary's paper. In fact, the digestive system of his so-called cercaria of *Diplodiscus temporatus* does not in reality correspond to that of the adult as his drawing and description suggest. Cary is also in error in his description of the tail of this cercaria, since the material which he sent me shows that it is much longer than he figures it and has a truncated end (Fig. 27). Neither does the reproductive anlage of this cercaria agree with his description and drawing (p. 606, Pl. 30, Fig. 6), for instead of three definitely circumscribed areas two in front of the acetabulum and one behind, it really consists of a small mass just in front of the excretory vesicle connected with a mass in front of the acetabulum by a line of nuclei.



When the adult *Diplodiscus temporatus* is compared with the larger of the cercariae which Cary assigns to it certain differences of structure are noted so fundamental that it seems impossible that the two forms can be the same species. Compare figures 27 and 28. The adult is a typical amphistome with the conical body terminating in a very large acetabulum, while the cercaria is widest toward the anterior end, flattened and its acetabulum which is only a little larger than the oral sucker is just back of the center of the body. Certainly very remarkable changes in shape and position of the organs would be necessary before the cercaria which developed in rediae in *Goniobasis virginica*, which Cary described, could metamorphose into an adult *Diplodiscus temporatus*. Cary makes no attempt to bridge this gap altho it would seem from his infection experiments that intermediate stages should have been obtained. It is especially hard to believe that the ventral sucker could have migrated from the middle of the body to the posterior end and have become so much larger in proportion to the oral sucker, and that the digestive system could have changed so fundamentally as would have been necessary. In those species of trematodes in which the development is known the digestive and excretory systems are very much alike in the cercariae and in the adults. The principal changes come in the development of the reproductive organs and the corresponding enlargement of body regions, usually the post-acetabular.

The infection experiments that Cary conducted to prove the connection between this cercaria and *Diplodiscus temporatus* seem convincing until they are carefully analyzed. To carry conviction they should have been better controlled, described in more detail and the stages of development worked out. That I may do Cary no injustice I will quote in full his account of the experiments that he used to prove the connection between the cercaria and the adult (Cary, 1909: 612-613).

"On Oct. 30 a number of tadpoles of *Rana catesbiana* were secured and several put in each jar containing infected snails. The tadpoles came from a pond in the grounds of the Biological Hall of the University of Pennsylvania, where *Goniobasis* is not found, so it seemed improbable that they would be infected with the parasite that was found about Princeton. As an added precaution all of the tissues of three of the tadpoles were carefully examined without finding parasites of any kind. When the tadpoles had been for a week in the jar containing the encysted cercariae, a dead individual was found. This one was examined for the presence of parasites with the following results: Nine worms, which from the condition of the sexual organs could be recognized as young, were found in the intestine of this tadpole. The other

organs of the body were entirely free from parasites. The worms in the intestine were about 2.5 mm. in length and 1 mm. in diameter at the posterior end. All of them were found in the last third of the intestine of the tadpole, scattered thruout that part of its length. During the time that they were under examination, as was also true in every other instance, the worms remained attached to the intestine of the host by a large posterior sucker. The anterior part of the body was in almost constant motion.

"Others of the tadpoles used in the experiment died from time to time and were examined for the presence of worms. The result of the examination was identical in every case. A greater or less number of worms, ranging from ten to thirty-one, was found in the posterior part of the intestine. In no case were any of the worms, or any other recognizable parasites, found in any of the other organs of the tadpoles.

"The intestines of two of the tadpoles at the time of death contained worms still within the cyst. Among the others, individuals of different ages could be recognized so it was definitely established that the tadpoles could serve as the host for the sexually mature worms.

"Since it seemed probable from the number of worms found in each of the dead tadpoles that they had in many instances been the direct cause of the death of the host, some larger tadpoles were secured for further experiments. These were put into jars containing encysted cercariae; but after they had remained there for a few days they were transferred to a jar in which there had been no snails. A tadpole from this jar was killed each week to note the development of the parasites. The conditions of the environment proved unfavorable for the tadpoles and the last one of them died on Jan. 19, 1909, after having been infected with *Diplodiscus* nine weeks. The worms which were taken from the intestine of this tadpole had fully developed sexual organs, but, so far as could be determined from the condition of the jar, no eggs had been laid, or at least no embryos had been developed."

An analysis of these experiments shows a number of weaknesses. The fact that the tadpoles came from a pond in the grounds of the Biological Hall at the University of Pennsylvania offers no check on the results. The location of the pond at Philadelphia and not at Princeton and the fact that *Goniobasis* does not occur there, can hardly be called evidence that *Diplodiscus temperatus* is not present in great numbers. The only check that Cary gives on his experiments is the examination for parasites of three tadpoles out of the whole lot. These he reports free from all parasitic infection. This does not prove that the others were uninfected. The three examined may have been without parasites while the rest were infected, or it is even possible that the

parasites may have been overlooked. Any man even if somewhat accustomed to examinations for parasites is likely to overlook them, especially if they are small and the infection light, until a chance finding directs his attention to a particular organ. Therefore it would seem that the above experiments were not sufficiently controlled to prove that no infection of *Diplodiscus temporatus* was present in the tadpoles previous to the experimental feeding.

For infection he puts the tadpoles in the jars with infected snails and when a week later one of the tadpoles proved to be infected with nine immature specimens of *Diplodiscus temporatus* he concluded that they had developed from the larvae in the snails. A comparison of the structure of the two forms shows how improbable this is. The largest cercaria of this type in the alcoholic material, which Cary sent me, had a body, 0.40 mm. in length and 0.20 mm. in width and an acetabulum 0.065 mm. in diameter. The only measurements that Cary gives in his description, which were evidently taken from a living specimen, are 2 mm. in length for both body and tail and 0.15 mm. in width. The tail is usually at least as long as the body, so that would make the body of the cercaria not over 0.1 mm. in length. Cary gives no measurements for the acetabulum but his drawing (Pl. 30, Fig. 6) shows it less than half the width of the body.

Since the cercariae must have had about the size, shape, and proportions given above at the time this tadpole was supposed to have eaten the cysts, their metamorphosis surely must have been extraordinary to have developed in a week into the immature specimens of *Diplodiscus temporatus*, which Cary found in the tadpoles. He describes these forms as 2.5 mm. in length, 1 mm. in diameter at the posterior end, and as being attached by the typical large posterior sucker. The posterior sucker of the young *Diplodiscus temporatus* (Fig. 28) has practically the width of the posterior end, which in this case would be almost 1 mm. Therefore if Cary's contention be correct his cercariae in one week almost tripled their length, changed the whole shape of the body, and increased their width five times. The acetabulum must in some way have jumped from the center of the body to the posterior extremity and increased its diameter ten times. Since such a transformation is impossible one is forced to conclude that the tadpoles used in the experiments were already infected with *Diplodiscus temporatus*, and that there is no connection between this species and the cercariae used in the experiment. The fact that according to Cary every tadpole examined was infected with *Diplodiscus temporatus* cannot be taken as attesting the success of the experiments but merely the general uniformity of the original infection. A detailed comparison of figures 27 and 28



shows how fundamental are the differences between the cercariae used in the experiments and *Diplodiscus temporatus*.

The second experiment is even less convincing than the first because no check whatever is given and the source of the tadpoles is not indicated, altho it is perhaps to be taken for granted that they are obtained from the same source as the first batch. These tadpoles were killed each week to note the development of the parasites and stages of *Diplodiscus temporatus* were found. If the development had followed the course that the writer maintains it would have been possible with this material to find transitional stages in change of shape, supposed migration of the acetabulum, etc. This Cary has not done and even the possibility seems to have escaped his notice, since it is not mentioned in the paper.

The following points have been proved in the above discussion.

1. That Cary described two entirely different species of cercariae as belonging to *Diplodiscus temporatus*;

- a. Those with stylets, which develop in sporocysts,

- b. Larger forms without stylets which develop in rediae.

2. That since the second type only were used in the infection experiments, no connection between the first type and *Diplodiscus temporatus* can have been shown.

3. That the infection experiments were not sufficiently controlled to be conclusive.

4. That the cercariae used could not have possibly developed into *Diplodiscus temporatus*, since the two forms differ so fundamentally in structure.

Since the stylet form of Cary's two species, which I have named *Cercaria caryi*, is very small, and no living material is available, it does not seem wise at the present time to attempt a detailed description. Figure 26 gives the most salient features. From the presence of the stylet, the small number of the stylet glands, and the small size of the acetabulum it may be placed with the Xiphidiocercariae in Lühe's group of the Cercariae microcotylae (Lühe, 1909: 196-198).

I was fortunate enough to obtain further material of the larger form, so that a detailed description of it is possible. On account of the great length to which the tail is sometimes stretched I shall describe it as *Cercaria megalura*.



## DISTOME CERCARIAE

The great bulk of known cercariae belong to this division. In my material are eleven distome cercariae representing eleven of the principal sub-groups.

## GYMNOCEPHALOUS CERCARIAE

Since beyond the fact that they develop in rediae the cercariae placed in this subdivision agree only in the absence of certain characters, it is without doubt an unnatural group. However in the present state of our knowledge it is convenient to retain it. Of my material only *Cercaria megalura* belongs here. This species and its allies differ so much from all the other cercariae of the gymnocephalous group, that I propose to make them the basis of a new sub-group, to which the name Megalurous or heavy-tailed cercariae may be given.

## MEGALUROUS CERCARIAE

From 73 specimens of *Pleurocera elevatum* from the Sangamon river near Mahomet, Illinois, examined during November and December, 1913, one was found with the liver packed with rediae in which developed a very peculiar kind of cercaria. Comparison showed this form to be the same as the larger cercaria which Cary assigns to *Diplodiscus temporatus*. Since Cary's account is not very complete, obscured by a mistaken viewpoint, and incorrect in many particulars, a further description of this species seems advisable. Altho many of the cercariae seemed fully matured, none were found free in the organs of the snail and no rediae were found which contained rediae.

Living rediae and cercariae of *Cercaria megalura* moved actively. The redia was very active and the region back of the posterior locomotor appendages on account of its mobility and attenuation resembled a tail. The anterior portion of the body also could be extended and contracted freely and with the aid of the locomotor appendages locomotion was possible. The cercaria was unable to use its tail for swimming in open water but on a substratum it moved fairly rapidly with the aid of the suckers. With the acetabulum attached the anterior end would reach out and the oral sucker take hold. The acetabulum would then loosen

its grip, and the body contract until the suckers were close together. The acetabulum would again take hold just back of the oral sucker, which would in its turn become loosened and extended. Locomotion consisted in a continued repetition of these movements. During this process the tail was contracted and took no part in the movement. At certain times a cercaria became attached by the posterior tip of the tail, which is furnished with an adhesive organ. The animal then extended to five or six times its usual length, and became greatly attenuated. While in this position the cercaria moved continually with a wriggling motion. Looss (1896:202) noted a similar activity in *Cercaria distomatosa* Sonsino from *Cleopatra bulimoides* Bourg., from Cairo, Egypt, a form very much like *Cercaria megalura*. This cercaria became attached by the extremity of the tail to the surface of the water or to some bodies such as plants or branches of trees very near the surface of the water, and moved in a serpentine manner like a tubificid worm. This comparison would apply equally well to *Cercaria megalura*. What relation this peculiar habit has to the future development of the cercaria is not known.

No cercariae were found encysting altho large numbers had extruded cystogenous material in the form of a sort of open tube around the body (Fig. 30). In fact this seemed to be the normal procedure when the animal came in contact with fresh water. Cary (1909:609-610) performed experiments with some of his specimens of *Cercaria megalura* which showed that this extrusion of cystogenous material was due to the change from the conditions in the liver of the snail to fresh water. Looss (1896:201-203) found no free individuals of *Cercaria distomatosa* in which the cystogenous material was still in the glands, and he also mentioned that when the cercariae were taken up in a pipette they became encysted as quick as a flash. He noted further that they encysted also in the open, loosening their hold and dropping to the bottom after having lived for a period free.

The redia (Figs. 31 and 36) of *Cercaria megalura* is an elongate sac slightly tapering toward the anterior end, with the posterior locomotor appendages about six-sevenths of the distance from the anterior to the posterior extremity. It is widest just in front of the appendages and tapers almost to a sharp point posteriorly. The birth pore is on the dorsal side just back of the pharynx.

The mouth of the redia is at the anterior tip and the oral cavity opens into a short, narrow passage, which widens out almost immediately into the voluminous digestive tract. This extends back of the posterior locomotor appendages nearly to the end of the body. In cross sections (Fig. 35) the intestine occupies from one-third to two-thirds of the body

cavity depending on the amount of food material present and the pressure from the developing cercariae. In the inner lining of the intestine were found flattened, scattered nuclei, but no cell boundaries could be distinguished. The body cavity occupies most of the entire region from just back of the oral sucker up to the posterior tip, but does not extend into the posterior locomotor appendages and the tail-like posterior extremity. These regions are filled with parenchymatous tissue in which definite cell boundaries could be determined (Fig. 35). The wall of the body cavity of even the youngest redia is very thin, and in the inner lining of flattened pavement cells with flattened nuclei, the cell boundaries could be distinguished only with difficulty. A small germ gland consisting of but few differentiated cells is present at the posterior extremity of the body cavity.

All ages of rediae were present in the snail from those in which the oldest contained cercaria was scarcely differentiated at all, to those in the body cavities of which there were from four to eight almost fully matured cercariae. The youngest redia studied (Fig. 36) which contained no cercariae having the cystogenous glands at all developed, was 0.53 mm. in length and 0.12 mm. in greatest width. The posterior locomotor appendages were 0.097 mm. from the posterior end, and the intestine extended to within 0.076 mm. of the posterior extremity. The pharynx was slightly elongated, being 0.049 mm. in length and 0.043 mm. in width. The body cavity contained a number of developing embryos only one of which was far enough along to be recognized as a cercaria. In this embryo (Fig. 36, cv) the tail was a mere stub hardly marked off from the body. The length of the body was 0.33 mm. and its width 0.054 mm., while the tail had a length of 0.038 mm. and a width of 0.032 mm. The sucker, digestive system, and reproductive anlage could be made out.

From one of the largest rediae studied the following measurements were taken (Fig. 31). The length was 1.16 mm., and the width 0.19 mm. The posterior locomotor appendages were 0.27 mm. from the posterior extremity, and the intestine, which filled about half the body cavity, extended to within 0.086 mm. of the posterior tip. There were four fully matured cercariae, one of which while still in the redia had extruded its cystogenous material, and a number of developing embryos of all ages. The pharynx of this redia was 0.054 mm. in length, and 0.049 mm. in width, showing almost no development in size from the very youngest redia.

The length and width of the body of *Cercaria megalura* (Figs. 29 and 30) vary greatly with the state of contraction. The tail varies from one-half the length of the body when the animal is moving on a



substratum to ten times that length when the cercaria is attached. The body is also about four or five times as long when extended as when contracted. At average extension the body is slightly pointed anteriorly and the acetabulum is but little more than half the distance from the anterior to the posterior end. The preacetabular region is a little wider than the postacetabular, and the postacetabular tapers slightly toward its truncated posterior extremity.

In mounted specimens the average length of the body is 0.4 mm., and the widest diameter of the preacetabular region averages 0.13 mm., while that of the postacetabular is 0.09 mm. The width of the tail at its base varies from 0.03 mm. to 0.054 mm., depending on the state of contraction. The oral sucker is lightly elongate, having an average length of 0.05 mm. and a width of 0.045 mm. The acetabulum is slightly larger and circular, averaging 0.054 mm. in diameter.

The structure of the tail of *Cercaria megalura* (Figs. 30 and 32) is interesting on account of its remarkable power of extension and the modification of its posterior end for attachment. It is truncated and there is an invagination at its tip. Into this inpushing open a clump of from 15 to 20 unicellular club-shaped glands. These glands have an average length of 0.017 mm. and width of 0.009 mm., and contain nuclei measuring 0.005 mm. in diameter. It is probable that these glands secrete some substance which makes possible the adhesion of the end of the tail. The tail is strongly attached at its base and except near the tip appears to be filled with vesicles, which are stretched out when the tail is extended and compressed when it is contracted. Figure 32 represents a cross section of the tail. The cuticula is very thin, the muscle layers reduced, and the great bulk of the tissue is made up of parenchymatous cells, the nuclei of which are surrounded by small masses of protoplasm. These cells are connected by strands of protoplasm and the large intercellular spaces which are filled with clear fluid give the appearance of vesicles. It is the looseness of the tissue of the tail which makes possible its remarkable changes in shape.

The cystogenous glands of *Cercaria megalura* are very highly developed and when the cystogenous material is still present in them they form the bulk of the whole body. These glands (Fig. 33 cs) are large, elongate, club-shaped cells, most of which open on the ventral surface, a few only opening dorsally. They are full of tiny, rod-shaped, cystogenous granules. The cells have an average length of 0.036 mm. and a width of 0.012 mm., and contain at about their centers large nuclei. They are present all thru the body of the cercaria from the posterior limit of the oral sucker almost to the posterior extremity. A comparison of cross sections of two cercariae at the region of the esophagus shows



the striking changes made in the glands and all the tissues by the extrusion of the cystogenous material (Figs. 33 and 34). The cystogenous glands in figure 34 have become much reduced in size, their cytoplasm is only slightly granular, and even their nuclei appear to have shrunk. In fact they are distinguished only with difficulty from the body parenchyma. The extruded material forms a layer about 0.0075 mm. in thickness, closely adhering to the animal. After the extrusion of the cystogenous material the cercaria becomes somewhat shorter, broader, and thinner than before.

The mouth of *Cercaria megalura* is subterminal and the oral cavity leads into a narrow prepharynx about the length of the oral sucker but varying greatly with the state of contraction. The pharynx is small, measuring on the average 0.022 mm. in length and 0.020 mm. in width, and opens by a narrow passage into a much wider portion of the esophagus. This soon divides into the narrow intestinal ceca which reach almost to the posterior end of the body. The lining of the enlarged portion of the esophagus and the intestinal ceca is formed by flattened pavement cells with flattened nuclei, which are illustrated in figures 33 and 34. Figures 29 and 30 both show the relations of the digestive system.

At the posterior end of the body is found the pyriform excretory vesicle which also has its walls formed of flattened cells with flattened nuclei. From the anterior end of the vesicle pass forward two longitudinal vessels which can be followed to the region of the pharynx (Fig. 30). The excretory pore was not distinguished. In *Cercaria distomatosa* Looss (1896:200) described the excretory system as having a short common trunk in the tail, leading from the bladder and opening to the outside by two short ducts. Cary in his material of *Cercaria megalura* located the excretory pore as dorsal just at the base of the tail, and found no extension of the excretory system into the tail. The most careful examination of the anterior part of the tail of *Cercaria megalura* in living specimens, toto mounts, and sections showed no trace of excretory tubules.

The anlage of the reproductive organs (Fig. 30 ra) appears as a small mass of nuclei just in front of the excretory bladder; from this a line of nuclei extends forward to join another small nuclear aggregation just in front of the acetabulum. No definite outlines of organs could be determined. The mass just anterior to the acetabulum represents to the ends of the reproductive ducts.

In the literature are found descriptions of only two cercariae resembling *Cercaria megalura*: *Cercaria distomatosa* Sonsino best described by Looss (1896:197-204), and a cercaria from the Hawaiian

Islands from *Melania baldwini* Annecy and *Melania newcombi* Lea, described briefly by Lutz (1893:327). Since in these forms there are no fixed larval organs such as spines, stylets, etc., to compare, specific differentiation is difficult. *Cercaria distomatosa*, however, seems to show some constant differences from *Cercaria megalura*. In *Cercaria distomatosa* the rediae reached a length of 1.8 mm., had a pharynx 0.07 mm. long, and a digestive system extending only to the posterior locomotor appendages, which are about three-fourths of the distance from the anterior to the posterior end. Also rediae were found in which rediae were developing. In *Cercaria megalura* as noted above the digestive system was more voluminous and reached almost to the posterior end of the body, and the posterior locomotor appendages were further back, being about six-sevenths of the distance from the anterior to the posterior end. Also Looss' measurements for *Cercaria distomatosa* are slightly larger than those for *Cercaria megalura*, and the judge from his figure and description, the tail is considerably smaller. He found the final tubules of the excretory system in the tail, which were not found in my species. The Hawaiian cercaria described by Lutz (1893:337) seemed to be similar to *Cercaria megalura* and *Cercaria distomatosa* in having a long tail by which it can become attached, in the general relationship of the body structures, and in the form of the cyst. A more detailed comparison is impossible on account of the meagerness of Lutz's description.

It is evident that these three forms are very closely related. Cary's attempt to relate *Cercaria megalura* to *Diplodiscus temporatus* is the only suggestion as to the life-history of a member of this group, but as shown above, this cannot be accepted.

#### ECHINOSTOME CERCARIAE

Cercariae belonging to the family *Echinostomidae* are very easily recognizable on account of their structural correspondence to the adults. It is impossible to subdivide them into smaller natural groups. The following may be given as a brief statement of characters for the Echinostome cercariae.

1. Distome cercariae developed in rediae.
2. Rediae have collar, birth-pore, and posterior locomotor appendages.
3. Cercaria with digestive system consisting of prepharynx, pharynx, long esophagus, and intestinal ceca reaching the posterior end of the body.
4. Anterior end of cercaria with collar and circle of spines.

5. Excretory system opening on each side of the anterior part of the tail; excretory bladder small, crura large, reaching to oral sucker.

6. Tail powerful, longer than body.

In the material used in this study were two echinostome cercariae.

The first species was found in several specimens of *Planorbis trivolvis*, examined during November, 1913, from a small pond near Urbana, Illinois. The infection consisted of rediae containing cercariae in the livers, and encysted cercariae in the body cavities of the snails. *Planorbis trivolvis* is then able to serve both as intermediate and secondary intermediate host for this species. I propose for this cercaria the name *Cercaria trivolvis*. The second of these larvae was found in a few out of thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut. The snails in this case I regard simply as the secondary intermediate host since no rediae were found. From the fact that the encysted cercaria had a pinkish tinge produced by pigment granules in the postacetabular region the name *Cercaria rubra* is proposed for this species.

*Cercaria trivolvis* (Fig. 39) completes its development before leaving the redia. Therefore very few cercariae were found free in the liver of the host. That a certain time is spent in free life is suggested by the fact that altho free swimming cercariae were kept under observation for a whole day none were seen to encyst. There seemed to be no connection between infection in the liver and cysts in the body cavity, since altho a few snails had both types of infection the majority had only one.

This cercaria (Fig. 39) moved actively both in open water and on a substratum. The tail was powerful and extended when the animal was swimming to two or three times the body length. For the swimming movement the cercaria bent ventrad almost double, with the posterior half of the body almost directly dorsad of the anterior. The tail which extended beyond the anterior end lashed vigorously and propelled the animal rapidly. When a cercaria came in contact with a surface it took hold with its suckers and moved actively with a creeping movement similar to that already described for *Cercaria megalura*. The structure and position of the crown of spines suggests that it would be of considerable aid to the animal in making its way thru connective tissue.

The cysts of this species were oval, having an average length of 0.16 mm. and width of 0.15 mm. The cyst wall varied in thickness from 0.007 mm. to 0.012 mm.

*Cercaria trivolvis* (Fig. 39) is elongate, pointed anteriorly, and has its greatest width in the region of the acetabulum. It has an heart-



shaped anterior end with a crown of thirty-seven spines. Well extended toto mounts have an average length of 0.38 mm. and a width of 0.12 mm. The tail is large and powerful in proportion to the size of the body, and in a state of average extension has a length of 0.50 mm. When contracted it may have a length considerably less than that of the body and when the cercaria is swimming it often reaches to two or three times that length. It ends in a sharp point and at the tip for about 0.05 mm. to 0.06 mm. it is narrow and is composed only of the muscle layers, lacking the parenchymatous core.

The oral sucker is almost exactly spherical and has an average diameter of 0.043 mm. The acetabulum is a little larger, being 0.049 mm. in diameter, and is situated two-thirds of the distance from the anterior to the posterior end.

The body from the anterior end to the acetabulum is set thickly with rows of small spines, only visible under the highest powers of the microscope.

The crown contains thirty-seven spines of equal size, arranged in two alternate rows, broken in the middle of the ventral surface. They are arranged regularly except for the two or three nearest the mid-line on the ventral side, which point in.

The body from the oral sucker to the attachment of the tail is filled with cystogenous glands. They are unicellular and club-shaped and all open on the dorsal surface.

The oral sucker is followed by a typical prepharynx about 0.022 mm. in length. The pharynx is round, on the average 0.017 mm. in diameter. The esophagus and intestinal ceca are not yet functional, but appear merely as columns of granules enclosed in membranes and containing irregular spaces representing the beginning of the lumina. The esophagus is long, reaching almost to the acetabulum, and the ceca reach nearly to the posterior end of the body.

*Cercaria trivolvis* (Fig. 39) has the typical echinostome excretory system. The portion in the tail was made out with great difficulty and is apparently not functional. A vessel passes back from the excretory bladder for one-fifth or one-sixth of the length of the tail and sends out two lateral branches which open to the outside. Dorsally at the base of the tail is the adult excretory pore which apparently at this stage gives passage to the outside for the waste material, since altho the vesicle kept filling and emptying the vessels of the tail did not change their caliber. In the oldest specimens the crura are large and distended from the bladder to the region of the pharynx with regularly-shaped, highly refractive granules. For the most part these are round or oval, but some of them appear to be compounded of from two to four of the



round ones. At the region of the pharynx the excretory tubules are much smaller and curve around forming a characteristic loop, from which a small vessel on each side could be traced back to the level of the acetabulum.

The nuclei which form the anlage of the reproductive organs of *Cercaria trivolvis* are not yet fully divided into separate masses. In the midline of the body just in front of the excretory bladder and behind the acetabulum is an elongate mass of these nuclei from which a line can be traced forward to a smaller mass in front of the acetabulum. The posterior mass probably develops into the ovary and testes, and the anterior mass represents the ends of the reproductive ducts.

Rediae of *Cercaria trivolvis* (Figs. 37 and 38) were present in the infected snails in various stages of development. The youngest were unpigmented but in the older ones orange colored pigment had developed in the outer wall, which rendered the largest rediae almost opaque.

The smallest redia found had a length of 0.30 mm. and a width of 0.065 mm. The posterior locomotor appendages were 0.22 mm. from the anterior end and the region back of them was attenuated and pointed. The oral sucker had a length of 0.041 mm. and width of 0.043 mm. and the intestine, which was very narrow and elongate, reached to the posterior locomotor appendages. No germ balls were present in the body cavity which was but little larger than the intestine, and the region of the germ gland was not visibly differentiated.

In a redia (Fig. 38) 0.41 mm. in length and 0.081 mm. in width the posterior locomotor appendages were 0.34 mm. from the anterior end. A ridge extended around the body like a welt 0.086 mm. from the anterior end. The body cavity at this stage had become well developed and contained germ balls, none of which however were in front of the posterior extremity of the intestine. The pharynx had a length of 0.043 mm. and a width of 0.046 mm. and the intestine, which was wider than the earlier stage and contained dark material, reached more than one-half the body length.

The great majority of rediae found were well advanced in development and contained mature cercariae in their body cavities (Fig. 37). The body cavity had increased in size extending from the birth-pore almost to the posterior end, and into the posterior locomotor appendages. In each redia were germ balls and from two to four mature cercariae, the bodies of which were from one-third to one-half the total length of the redia. In a mature redia 0.81 mm. in length and 0.15 mm. in width, the posterior locomotor appendages were 0.62 mm. from the anterior end. The pharynx was 0.041 mm. long and 0.043 mm. wide and the intestine which was somewhat distended with food material and

pushed ventrad by the cercariae, extended for more than one-third of the length of the body.

The pharynx is about the same size in the youngest and the oldest rediae, and the actual size of the intestine differs but little, altho its ratio to the size of the body is much less in the older form. The birth-pore is located on the dorsal side of the body a little back of the pharynx. In the oldest rediae the anterior collar is not present and the posterior locomotor appendages are much reduced.

Cysts of *Cercaria rubra* (Fig. 41) were present in the tissue above the gills of six of the thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut. The cysts were large, round, thick-walled, and of very uniform size, measuring 0.195 mm. to 0.205 mm. in diameter. The cyst wall was transparent and had a thickness of 0.016 mm. The worm almost completely filled the cyst with practically the whole dorsal surface against the wall, and the posterior end overlapping the anterior.

Several cysts were opened and the worms freed. A study was made of these while living but none were preserved.

The living cercariae (Fig. 40) were on the average 0.50 mm. in length and 0.15 mm. in width at the region of the heart-shaped anterior end. They tapered slightly posteriorly, had a width at the acetabulum of 0.13 mm. and the end was bluntly rounded.

The oral sucker of *Cercaria rubra* was a most exactly round having a transverse diameter of 0.043 mm. and the acetabulum which is two-thirds of the distance from the anterior to the posterior end was larger, measuring 0.065 mm.

The collar which is typical of the Echinostomes is very well defined in this species and has arranged around its edge in two alternating rows, forty-three spines, which vary only from 0.018 mm. to 0.022 mm. in length. In the middle of the ventral surface as is usual there is a depression and a break in the rows of spines. The four median spines on each side of this space are not in regular line with the others and point inward. Besides these eight there are seventeen spines in the upper row and eighteen in the lower row (Figs. 40 and 42). The surface of the body as far back as the acetabulum was covered thickly with rows of spines pointing backward. They were 0.005 to 0.007 mm. in length. The rows were 0.008 mm. apart and the spines were set thickly in the rows.

The digestive system (Fig. 40) offered nothing peculiar. The pre-pharynx had a length about equal to the diameter of the oral sucker, and the pharynx had a diameter of 0.025 mm. The short esophagus and

intestinal ceca contained the granules and their regular spaces described for *Cercaria trivolvis*.

Only the main branches of the excretory system could be traced. The crura were packed very full of concretions and the bladder was narrow.

Since this species was only studied alive the anlage of the reproductive system could not be distinguished.

In comparison with the large numbers of adult Echinostomes known the descriptions of but few larval forms are to be found in the literature. *Cercaria rubra* differs markedly from all of these in the number and arrangement of the oral spines. *Cercaria trivolvis* on the other hand agrees very closely with *Cercaria echinata* von Siebold. This form is not sufficiently described to make a detailed comparison possible. Lühe (1909:188) gives to it thirty-seven spines of equal size in the crown, altho the earlier writers counted only thirty-six. The intestine of the redia is shorter in *Cercaria echinata* than in *Cercaria trivolvis*, and the size of the oral sucker in comparison to the acetabulum is less in the former than in the latter species.

A number of suggestions have been made in regard to the adults corresponding to the European species of echinostome cercariae. None of these proposed relationships have been proved by experiments. Lühe (1909:65) recently made the following statement in regard to this group:

“von den bisher mit Namen unterschiedenen Cercarien (sämtlich aus Süßwasserschnecken) ist noch keine mit volliger Sicherheit auf eine bestimmte Art zu beziehen.”

In England two echinostome cercariae have been assigned to adults on the basis of morphological comparisons. The cercariae were not given special names; the adults are *Echinostomum leptosomum* Creplin by Lebour (1907:447-451) and *Echinostomum secundum* Nicoll by Nicoll (1906:517-518).

None of the adult echinostomes from North America agree in the number and arrangement of the anterior spines with the two cercariae described above.

The following form, for which I propose the name *Cercaria reflexae*, and which was found in, some of the specimens of *Lymnaea reflexo* from Chicago, Ill., will be treated as an appendix to the Echinostome cercariae. The livers of the snails infected with *Cercaria reflexae* were packed with rediae in various stages of development of which the greatest numbers were large and full of numerous mature cercariae. Sections of the liver showed that but very few cercariae were free in its tissues but large



numbers were freed when the organ was removed from the snail. Also in the body cavities of numbers of the same snails were found encysted cercariae of the same species. That the cercariae were continually making their way out and encysting in new snails was shown by the fact, that while during the first few days after the snails came into the laboratory only a few contained the encysted cercariae, later all were infected.

The movement of *Cercaria reflexae* both in open water and in a substratum was exactly like that of *Cercaria trivolvis*.

The body varied greatly in size and shape. When contracted for locomotion it was nearly as wide as long. A fairly well extended mounted specimen (Fig. 43) is pointed anteriorly, widest at about the level of the acetabulum and narrower at the posterior end. The anterior end does not suggest the echinostome collar, and there is no crown of spines. One well extended specimen had a length of 0.46 mm. and a width at the acetabulum of 0.135 mm., with a thickness of a little more than half the width.

The tail at average extension has a length a little greater than the body, and an average width at its base of 0.05 mm. to 0.06 mm. The tail is provided with a dorsal and a ventral fin-like ridge which is narrow at its base and at its widest part equals about one-half the diameter of the tail.

The oral sucker has a diameter of 0.046 mm. and the acetabulum which is just back of the middle of the body is 0.06 mm. in width.

The surface of the body back to the region about half way from the acetabulum to the posterior end is covered with small spines arranged in rows and set closely together.

The whole body from the oral sucker to the posterior extremity contains large unicellular cystogenous glands which open dorsally, and fill the bulk of the body toward the dorsal side. These are like the cystogenous glands already described for *Cercaria megalura* and the amphistomes.

The oral cavity is followed by a short prepharynx and a small pharynx, 0.022 mm. in diameter. The esophagus and the intestinal ceca were very small and could only be followed in sections. The esophagus reaches almost to the acetabulum and the intestinal ceca to the posterior end.

The excretory system of *Cercaria reflexae* (Fig. 43, ex) is very much like that of *Cercaria trivolvis*. In the former species the vessels from the bladder to the tail are larger and serve to carry away the excretory products, for when the excretory bladder became contracted they became distended but soon again became reduced. The excretory crura too are smaller than in the other species. Opening into the



crura could be traced smaller vessels leading from the posterior end of the body, and forming a loop at the region of the pharynx similar to that of the echinostomes.

The nervous system shows very prominently both in living and preserved specimens and its larger branches can easily be traced. It shows nothing peculiar. From the large masses on each side of the prepharynx two branches pass out to the oral sucker. Laterally there are two branches on each side in the pharyngeal region, and strands can be traced almost to the posterior end of the body.

That the specimens of *Cercaria reflexae* which came under my observation were well along in development is attested by the condition of the reproductive anlage (Fig. 43). It is divided into four definite areas. In the region of the mid-line just in front of the excretory bladder are three masses of nuclei, one in front of the other and close together. The posterior two which are smaller than the other probably represent the anlage of the testes, while the anterior larger mass of nuclei the anlage of the ovary and the structures surrounding it. Just in front of the acetabulum is a mass of nuclei representing the future ends of the reproductive ducts. The course of the ducts connecting these areas could not be traced.

The rediae of *Cercaria reflexae* (Fig. 45) were present in different stages of development in the infected snails, altho there was a great preponderance of the fully matured forms. The smaller rediae were very active in extending and contracting their bodies, and were able to make progress with the aid of their posterior locomotor appendages. The largest forms were sluggish and reduced to mere sacs containing cercariae.

The smallest rediae have much the same structure as those of *Cercaria trivolvis*. One of them measured 0.28 mm. in length and 0.054 mm. in width and had the posterior locomotor appendages 0.22 mm. from the anterior end. The anterior ridge or collar was very prominent, 0.022 mm. from the anterior end, and the pharynx had a diameter of 0.043 mm. A number of small germ balls were present in the body cavity and the intestine extended to the region of the posterior locomotor appendages.

A redia somewhat larger than the one just described is shown in figure 44. In this form the cercariae are beginning to be developed into recognizable form.

The nervous system was quite well developed in the young rediae of this species. In one very immature specimen studied while alive two large nervous masses (Fig. 46, n) could be distinguished on each side of the posterior part of the oral sucker, which sent two branches

forward and two backward soon to become lost in the body wall. Very few observations on the nervous system of the rediae are found in the literature. Looss (1896:199) traced the nervous system of the rediae of *Cercaria distomatosa* about as far as it is followed in the above description. He speaks of this as the best developed of the nervous systems described in the rediae up to that time. The degree of development of the nervous system as he suggests is correlated with the degree of mobility of the rediae.

In the largest of the rediae (Fig. 45) almost all the germ balls have developed into mature cercariae, of which from twenty to thirty are present. The body cavity is much enlarged, the cercariae having pushed clear into the posterior tip, into the posterior locomotor appendages and up around the oral sucker. The rediae are mere shells, the anterior collar having been obliterated and the posterior locomotor appendages much reduced. The length of one of the largest rediae found was 2.26 mm., the width 0.30 mm. and the posterior locomotor appendages were 1.65 mm. from the anterior end. The oral sucker is very little different in size from that in the younger specimens, its diameter being 0.056 mm. The intestine was long and slender and reached to a point 1.15 mm. from the anterior end.

That *Cercaria reflexae* is closely related to the echinostomes is shown by a comparison with *Cercaria trivolvis*. The rediae of the two species have much the same general structure. In fact it would be practically impossible to distinguish between very young rediae of the two forms. Further, the locomotion and general body structures of the two cercariae are similar. The arrangement of the anlage of the reproductive organs of the two forms is much alike. That *Cercaria reflexae* is simply an immature echinostome cercaria in which the crown of spines has not developed is improbable from the fact that its other structures are those of a well advanced cercaria, the anlagen of the reproductive organs especially being considerably differentiated. No record has been found of any species either cercaria or adult which agrees with *Cercaria reflexae*.

#### MICROCERCOUS CERCARIAE

Among thirty-six specimens of *Campeloma subsolidum* from Hartford, Connecticut, four were found to be infected with rediae and very short tailed cercariae. The infection was in the tissues of the body above and at the bases of the gills. This form, which has a very short triangular tail, I propose to name *Cercaria trigonura*.

The cercariae were free in the tissues of the snail, were numerous, and were all in the same stage of development. When freed, they ex-

tended and contracted their bodies rapidly, the preacetabular region being the most active, but they were unable to swim. The tail, bent ventrad and pushing against the substratum, aided somewhat in locomotion, and at times the oral sucker was used for attachment. By this peculiar method the animal was able to make a little progress with a great deal of effort. Leuckart (1886:86) notes the same type of movement for *Cercaria limacis* Moulinié, a stumpy tailed cercaria from *Limax cineria*.

“Ausser Stande zu schwimmen, benutzen diese Wurmer den fast hertzformigen Schwanzanhang beim Kriechen als Nachschieber.”  
Some of these cercariae were kept alive and active in tap-water for three or four days.

*Cercaria trigonura* (Figs. 48, 50) has an elongate, cylindrical body, averaging in mounted specimens 0.24 mm. in length and 0.06 mm. in width. The oral sucker measures on the average 0.049 mm. in length and 0.039 mm. in width and the acetabulum which is slightly back of the center of the body is smaller, being 0.04 mm. in diameter. The cuticula is thin and at the anterior end beset with tiny spines, which are numerous over the oral sucker, thin out posteriad and disappear entirely back of the pharynx.

The tail of *Cercaria trigonura* is short, easily detached, grooved ventrally, and has the extremity bluntly pointed (Figs. 48, 50). It has an average length of 0.052 mm. and a width of 0.024 mm. Under the cuticula is a thin layer of circular muscles which are supplemented ventrally by a number of stronger longitudinal fibers that extend from the base to the tip. The size of these strands and the fact that they have no opposing muscles on the dorsal side would account for the fact that the tail is usually bent ventrad. The bulk of the tail is formed of loose parenchymatous tissue consisting of scattered nuclei, connecting protoplasmic strands and good sized vesicles.

On the ventral surface of *Cercaria trigonura* just at the base of the tail is a slit-like opening, which extends forward a short distance and dorsad reaches up into the body. Opening into this cavity are large numbers of unicellular glands which stain very heavily with haematoxylin. Figure 48 pg shows the relation of this posterior glandular structure. It is interesting that the shape and position of the tail give it the appearance of a short trough ready to carry off the secretions of this gland. The position and structure of the posterior gland suggest that it may function for adhesion. No activity which suggests such a function has been observed and for none of the other stumpy tailed cercariae has the description of a posterior glandular structure been found.



Set in the dorsal part of the oral sucker and protruding for about one-fifth of its length is a cephalic spine or stylet (Figs. 47, 49). The spine has a length of 0.018 mm. and a width of 0.004 mm., is sharply pointed and slightly thickened about two-thirds of the distance from the base to the tip. Ventrally no thickening is present.

The cephalic or stylet glands (Fig. 48, sg) fill the space dorsad and anterior to the acetabulum and extend forward to just back of the nervous system. The individual glands are small, averaging 0.024 mm. in length and 0.012 mm. in width, finely granular and contain small nuclei. Their ducts pass forward dorsally over the oral sucker and open around the cephalic spine in the anterior pit. The numbers were so large that no accurate count could be made. They form a single mass unbroken in the median line.

The mouth is subterminal and back of the oral sucker is a small pharynx, 0.012 mm. in length by 0.01 mm. in width. The prepharynx is short and the esophagus and intestinal ceca are entirely undeveloped.

The excretory pore of *Cercaria trigonura* opens dorsally at the posterior extremity of the body just at the base of the tail. Leading up to it is a narrow tube near the dorsal surface which expands into the large bicornuate excretory vesicle, the horns of which reach on each side of the acetabulum. Vessels could be traced along the sides of the body from the tips of the horns of the vesicle up to the pharynx. Figures 48 and 50 give the relations of the pore vesicle and vessels. The vesicle is lined with a thick layer of granular, cuboidal, epithelial cells with large nuclei (Fig. 54, ex). An excretory vesicle with thickened walls of the character just described has been found in the other so-called stumpy-tailed forms.

The anlage of the reproductive organs shows as a mass of nuclei dorsal to the posterior part of the acetabulum (Fig. 48, ra).

Along with the cercariae in the tissues of *Campeloma subsolidum* were large numbers of rediae of different sizes. They were found in every snail infected with *Cercaria trigonura* and were not found in any instance where this species was not present. The only rediae that showed any activity were very small immature forms which were present in considerable numbers and in the same stage of development. They were active, extending and contracting and twisting and turning in all directions. Part of them were sharply pointed and the others bluntly rounded posteriorly. The first type (Fig. 51) was the most common and the structure of these will be described in some detail. The average of the mounted specimens of the small rediae is 0.019 mm. in length and 0.04 mm. in width. The pharynx is small, 0.03 mm. in width



and set back slightly from the anterior end so that the anterior part of the oral cavity is in front of it. The intestine is narrow and elongate reaching nearly to the end of the body and almost filling the small body cavity. Inside of the cuticula and muscle layers the wall is made up of embryonic nuclei with poorly defined cell boundaries. There are present no developing embryos and the germ gland is not clearly differentiated.

Very few rediae were found showing intermediate stages between the small type just described and the largest forms. The one shown in Figure 53 with only five germ balls of any size in its body cavity is 0.43 mm. in length and 0.09 mm. in diameter. The pharynx has the same width as length, 0.043 mm., and the pouch shaped intestine, which is 0.11 mm. long and 0.038 mm. at its greatest width, extends to a point only about one-third of the distance from the anterior to the posterior end. The body cavity is large and contains oval germ balls, the largest of which is 0.076 mm. long and 0.06 mm. wide. The wall of the cavity is about two cells thick and the germ gland is clearly defined containing both single germ cells and balls of several cells. The pharynx in this form is also set back from the anterior end.

The largest rediae (Fig. 52) are all rounded at their posterior extremities and their body cavities are very large with thin walls. The germ gland is much reduced. At one side near the anterior end is located the birth pore with protruding lips. The rediae vary in size up to the largest measured which is 0.73 mm. in length. The largest ones have from 25 to 30 germ balls of about the same size in their body cavities. The intestine is smaller in proportion to the size of the body but of about the same absolute size as in the smaller forms, and the oral sucker is very clearly set back from the anterior end. The outer layers at the anterior part are wrinkled so that the appearance is given of a series of horizontal folds from the anterior tip back to the middle of the body.

Besides the large rediae with the body cavity full of germ balls there are present numbers of large rediae with few or no germ balls and much constricted and twisted.

That these rediae are the nurse generations of *Cercaria trigonura* is very probable from their being found in every instance with that form. All the most immature rediae are about the same size and appear to belong to the same brood, yet there is no evidence as to their origin. Neither is there any evidence where the cercariae free in the tissues come from, for in none of the rediae can cercariae be distinguished. The old rediae shells may have been the nurses of these cercariae and rediae but even when a few embryos are found in these, they are merely large little differentiated germ balls. It is possible that in these snails

were represented several infections and that the approach of winter, for the examinations were made in November, may have arrested the development of the second brood.

The only possible group in Lühe's (1909) classification of the cercariae where *Cercaria trigonura* might fit is with the Microcercous cercariae. An analysis of the forms coming under this category shows that they cannot form a natural group. Dollfuss (1914) in the preliminary account of his work on this group separates from it the Cotylocercous cercariae which he considers to be a natural subdivision.

He gives the following characters for the Cotylocercous cercariae.

1. Cercariae developing in simple sporocysts parasitic in marine gastropods.

2. Oral sucker with stylet; stylet glands fill a large part of the anterior region of the body.

3. Bladder large not bifurcate occupying almost all the posterior region of the body; wall formed by a single layer of large granular cells, which have the appearance of glands.

4. Tail very short, wide at least at its base, consisting of a cup with thick walls of large cells, which functions as a sucker.

Dollfuss is in doubt in regard to the specific distinctness of some of the members of this group. He therefore designates them together provisionally under the name *Cercaria pachycerca* Diesing "sensu lato et var." Under this designation he includes *Cercaria brachyura* Lespes, *Cercaria cotylura* Pagenstecher, and several new forms. Besides these are included in the Cotylocercous cercariae as undoubtedly distinct species *Cercaria linearis* Lespes and *Cercaria buccini* sp. inq. Lebour. Dollfuss states in regard to this group that the cercariae are so alike in structure that the adults must be closely related.

Aside from the cercaria of *Catoptroides macrocotyle* Lühe (*Phyllostomum folium* Ssinitzin) and metacercariae, which have been related to the Microcercous cercariae without any good reason, there are left after the separation of the Cotylocercous cercariae, five more or less well known forms.

1. *Cercaria limacis* (Moulinie' (1856:83, 163-164) from sporocysts in the terrestrial molluscs *Arion rufus* L. and *Limax cinereus* O. F. Müller.

2. *Cercaria micrura* de Filippi (1857:5-7) (larva of *Sphaerostomum bramae* (O. F. Müller) from sporocysts in the freshwater snail *Bithynia tentaculata*.

3. *Cercaria myzura* Pagenstecher (1881:25, 26) from rediae in the fresh-water molluscs *Neritina* (*Theodoxia*) *fluviatilis* L.

4. *Cercaria trigonura* mihi from rediae in the fresh-water snail *Campeloma subsolidum*.

5. *Cercaria columbellae* Pagenstecher (1862:305-306) from rediae in the marine molluscs *Columbella rustica* L.

Of the two of the above cercariae developed in sporocysts only *Cercaria micrura* agrees in structure with the characters given for the Cotylocercous cercariae. The only reason for not including it in this group is apparently that it is a fresh-water form. Just why it should be excluded from this group for this reason when it agrees with them in structure is not clear.

*Cercaria myzura* Pagenstecher, *Cercaria columbellae* Pagenstecher, and *Cercaria trigonura* mihi are the three stumpy-tailed forms which develop from rediae. Two are from fresh-water and one is marine. Both of Pagenstecher's forms are so insufficiently known that but little structural comparison is possible. *Cercaria myzura* and *Cercaria columbellae* both have the truncated tail like Cotylocercous group.

*Cercaria trigonura* is unique among the stumpy-tailed forms in having a large posterior gland opening at the base of the tail and a bicornuate excretory vesicle. It differs from all except Moulinie's (1856:-83, 163-164) *Cercaria limacis* in having a blunted tail, which is not modified as a sucker.

#### FURCOCERCOUS CERCARIAE

Sporocysts containing small forked-tailed cercariae with eye-spots, were found in five out of thirty-eight specimens of *Lymnaea reflexa* from a small pond in the suburbs of Chicago, Illinois. I propose to name this form *Cercaria douthitti*.

The livers of the snails infected with *Cercaria douthitti* were filled with a tangled mass of elongate, cylindrical sporocysts. The walls of the sporocysts were so thin and in such close contact with the liver lobes (Fig. 63, sw), that it was impossible to free individual sporocysts and to follow them to any length. They were irregular tubes of varying caliber, had no free, mobile, club-shaped ends sticking out, and were filled with large numbers of embryos in various stages of development. (Fig. 64). The walls of the sporocysts were made up of a very thin fibrous layer on the inside of which were scattered nuclei (Fig 63).

None of the cercariae were found outside of the sporocysts in the snail, but when the liver was dissected large numbers worked their way out. Their progress from place to place was quite erratic altho they moved their bodies and tails vigorously. When in locomotion the body and tail were both somewhat contracted and both moved back and forth.



The movement of the tail was not a lashing as in many forms, but a vibration in which the middle region was the most active. The cercaria kept catching hold with its acetabulum and extending its anterior end, but was not able to take hold with the oral sucker, which even in the older specimens was not fully developed. Sometimes when a cercaria under observation was pressed lightly with a cover-glass it would catch hold with the ventral sucker and the vibrations of the tail would cause it to swing round and round on the sucker as pivot.

*Cercaria douthitti* is a very small form, cylindrical in cross section, slightly wider at the center and tapering from the acetabulum to the posterior end to a width equal to about that of the tail. The body has an average length in well extended mounted specimens of 0.19 mm. and a width of 0.067 mm. The tail is bifid and even when contracted is equal to about one and one-half the length of the body. The lobes form less than one-third of its length and are definitely constricted from the main portion, making the tail appear as if jointed (Fig. 55). The main stem of the tail has an average length of 0.22 mm. and a width of 0.025 mm., while the lobes have about half that width and an average length of 0.089 mm. When the cercaria is alive the tail has a range of variation from less than once to about twice the length of the body. Underneath the thin cuticula and the muscle layers of the tail is a layer of unicellular club-shaped glands(?), which lie close together and have their ducts extending forward to open to the outside along the sides. These glands were only seen in the living specimens. The central core of the tail is composed of parenchymatous tissue, thru which flows the caudal branch of the excretory system. The base of the tail fits into a depression at the posterior end of the body, which is open ventrally (Fig. 57).

The oral sucker of *Cercaria douthitti* is proportionally large, measuring on the average 0.057 mm. in length and 0.045 mm. in width. It is a mass of embryonic cells which are separated from the surrounding tissue by a fibrous sheath, except that the ducts of the cephalic glands pass thru to open at the anterior tip. There is no differentiation into muscle fibers and no mouth or oral cavity is marked. *Cercaria ocellata*, a European forked-tailed form which corresponds in structure very closely to *Cercaria douthitti* is described as having a definite mouth opening, by La Valette St. George (1855:22-23). He also gives measurements much smaller for the oral suckers than those of *Cercaria douthitti*, making it less than half as large as the acetabulum (0.013 mm. to 0.033 mm.) Lühe (1909:206) questions his measurements, and since in La Valette St. George's drawing that region is not clear, it may well be that he did not grasp the true proportions of the oral sucker, and that it is as



large in his form as in *Cercaria douthitti*. The acetabulum is fully functional as noted above. It is very small, on the average 0.025 mm. in diameter, situated just back of the middle of the body.

The eye-spots are in front of the middle of the body and located nearer the dorsal side. The pigment masses which compose them are in the shape of concavo-convex discs, 0.007 mm. in diameter, placed so that the concave surfaces are toward the sides of the body. Fitting into the concave side of each is a small lens. In the region of the eyes and lying just ventrad and behind them is the central nervous system. A cross section of the cercaria in the region of the eye-spots brings out these relations clearly (Fig. 56, e).

The region back of the center of the body of *Cercaria douthitti* is almost completely filled with large unicellular cephalic glands, the usual number of which is eight. The most anterior reach to the middle of the body and from all, large ducts extend forward in two groups. These two groups of ducts pass thru the sheath of the oral sucker posteriorly and traverse this organ to open at the anterior tip of the body (Fig. 59, 60, 61, 62). No cephalic spine is present altho these glands appear to be analogous to stylet glands. *Cercaria ocellata* La Valette St. George (1855:22-23) is the only other furcocercous cercaria in which such glands are described. The glands are flasked-shaped and have a length varying from 0.04 mm to 0.05 mm. and a width of from 0.025 to 0.03 mm. The thickness is about equal to the width. A traverse section (Fig. 58) thru the acetabular region of *Cercaria douthitti* shows how much of the body space is taken up by the cephalic glands.

At the posterior end of the body of *Cercaria douthitti* is a small excretory vesicle from which two crura could be traced forward only as far as the acetabulum. Backward from the bladder two small vessels pass into the tail (Fig. 57, ex). These soon unite into the central caudal vessel which divides to run down the lobes and opens at their tips (Fig. 55). No concretions of any kind were present in the excretory system.

Just in front of the excretory bladder and wedged between the tips of the cephalic glands, is a small mass of nuclei the anlagen of the reproductive organs.

The furcocercous or forked-tailed cercariae are very imperfectly known. The anatomy of only a few of the known forms is at all well worked out and the life-history of no one of them has been determined. At least a dozen species have been reported as distinct, some of which, however, have been described very briefly in the older accounts. Sufficient evidence is not available to justify any conclusion as to the natural or artificial character of this group.

Only one of the forked-tailed cercariae, *Cercaria ocellata* La Valette St. George corresponds at all closely in structure to *Cercaria douthitti*. The structure of this form has been fairly well worked out by La Valette St. George (1855:22-23) and Moulinié (1856:172-173). *Cercaria ocellata* agrees with *Cercaria douthitti* in the large unicellular glands of the posterior body region, in the presence of eyespots, in the length and jointed character of the tail, and in fact that the forked portion is only one-third of its total length. The ratio in size of the suckers may agree as stated above.

*Cercaria ocellata* differs in several particulars from *Cercaria douthitti*. The former is almost twice as large, is found in a different host, in a different continent, and has narrow fin-like extensions on the divided lobes of the tail.

No suggestion can be made as to the life-history of *Cercaria douthitti*. Its structure is such as not even to suggest to what family of distomes the adult belongs. In fact hardly a suggestion has been made in regard to the life-histories of the forked-tailed cercariae and no experiments that I can find have been carried on to trace their development. Certainly further studies are needed on their structure and development.

#### XIPHIDIOCERCARIAE

Lühe (1909:189) defines Diesing's (1855) group of the Xiphidio-cercariae or stylet cercariae as follows:

Slender-tailed distome cercariae with a boring spine on the rounded anterior end. Eyes lacking; develop in sporocysts; encystment in a secondary intermediate host.

Since this group is formed on likenesses in but few larval characters it can be considered only within wide limits as expressing relationship. On account of their small size and also since many of them are known only from the older accounts many of the forms of this group are very insufficiently described. Five new forms are added to this group by the study of my material. In the following account the new American forms will be compared with the most closely related of the already known species, and where it is possible an attempt will be made to fit them into natural groups.

Two of these forms with the related European species agree so closely in structure that a new group, the Polyadenous cercariae will be formed for them.

## POLYADENOUS CERCARIAE

In eighteen per cent., of 170 specimens of *Planorbis trivolvis* collected from the drainage ditch north-east of Urbana, Illinois, the livers were filled with elongate, cylindrical sporocysts very much twisted together. The sporocysts were not branching but it was very difficult to trace out the individual sacs. When this could be done they were found to be of about uniform caliber and various lengths (Fig. 66). Two that were measured were 1.48 mm. and 1.9 mm. in length and varied in diameter from 0.13 mm. to 0.17 mm. The walls were thin and contained flecks of orange pigment, which were very dense in the oldest specimens. Many of the sporocysts contained large numbers of actively moving cercariae which would escape and swim about freely when the liver was teased apart. The wall of the sporocyst was composed of a layer of pavement epithelium with flattened nuclei. No thickenings were found in the wall and no traces of germ gland, although small germ balls were free in the cavity. Cercariae at all stages of development were found in the sporocysts (Fig. 65). I propose to call this species *Cercaria isocotylea* from the fact that the acetabulum and the oral sucker are very nearly equal in size.

*Cercaria isocotylea* (Fig. 68) is oval elongate, slightly pointed anteriorly, and of uniform width from the region of the pharynx back to the acetabulum. The length and the width varied with the contraction state within rather wide limits. From the measurements of mounted specimens of moderate contraction, the length averages 0.17 mm. and the width 0.06 mm. The cross section is oval and the thickness a little greater than half the width. The tail is small in proportion to the size of the body and set in a groove on the ventral side of the posterior end. When contracted it may be less than one-half the body length, but when the cercariae is swimming it may be extended to greater than that length. Under ordinary circumstances it has an average length of 0.01 mm. and a width at its base of 0.02 mm.

*Cercaria isocotylea* moved actively both in open water and on a substratum. When swimming it turned so that the ventral side was up, the body was contracted and bent slightly ventrad. The tail became much extended and lashed rapidly backward and forward. It did not however have the power of moving the animal definitely in one direction for any length of time, and locomotion was very erratic. Whenever while swimming the cercaria came in contact with a surface, the tail ceased its lashing and the body began to stretch and reach around until the oral sucker could obtain a hold. Then the animal would creep along with the aid of its suckers. Sometimes after the cercariae had come



in contact with a surface and extended its body, the tail resumed its lashings and swimming was started again with the body extended. This was simply preliminary to the contraction of the body and the resumption of the usual swimming position.

The oral sucker of *Cercaria isocotylea* (Fig. 68, os) has an average length in mounted sections of 0.04 mm. and a width of 0.037 mm., while the acetabulum which is spherical in the living animal, is about two-thirds of the distance from the anterior to the posterior end and has a diameter of 0.036 mm.

Set in the dorsal wall of the oral sucker is a large sylet (Fig. 67) which is sharp pointed and has a thickening two-thirds of the distance from its base to its tip. It is flattened ventrally, has a length of from 0.028 mm. to 0.030 mm. and a width at its base one-sixth of its length.

The whole surface of the body back to the anterior margin of the acetabulum is thickly set with tiny cuticular spines which are 0.003 mm. to 0.004 mm. in length. Back of this region the cuticula is entirely smooth.

On each side of the stylet open the ducts of the stylet glands, which form a group on each side. The glands are elongate, sac-shaped, unicellular and faintly granular, with a length of from 0.02 to 0.025 mm. and a width of from 0.011 to 0.013 mm. They form two clumps of from six to eight in a clump, in the region just in front and to each side of the oral sucker.

In this stage of development of the cercariae no cystogenous glands are present.

Except for the mouth, oral cavity, very short prepharynx, and pharynx the digestive system of *Cercaria isocotylea* is undeveloped. The mouth is very small having a transverse diameter of 0.012 mm. and the round pharynx is 0.016 mm. in width.

The excretory pore opens on the dorsal side just at the base of the tail. The bladder is bicornuate consisting of a median part and two lateral horns which reach on each side up to the middle of the acetabulum. From the anterior and posterior regions on each side can be traced small vessels which unite into a short common duct to open at the tips of the horns. (Fig. 68, ex)

The anlage of the reproductive organs is not divided into definite parts. It consists of a mass of small nuclei which lies dorsad and just in front of the anterior margin of the acetabulum. This connects with a larger mass which is dorsal to the posterior part of the acetabulum by a broad band running around dorsal to the left margin of the sucker.

Among the specimens of *Lymnaea reflexa* from Chicago was one which contained a number of elongated unpigmented sporocysts, which



were found in the liver with the rediae of *Cercaria reflexae*. These sporocysts were much like those of *Cercaria isocotylea*, and were so thin walled and so closely interwoven with the lobes of the liver that none were isolated for accurate measurements. Altho large numbers of the cercariae in the sporocysts were mature, few were free in the liver of the host. When, however, the liver was taken out of the snail many were freed and swam actively about. I propose the name *Cercaria polyadena* for this species from the fact that the body of the cercaria contains such large numbers of gland cells.

The position of *Cercaria polyadena* in swimming was similar to that of *Cercaria isocotylea*. The tail was, however, somewhat stronger than in the latter species and the animal was able to move forward definitely and fairly rapidly. Whenever the cercaria came in contact with a surface, it immediately settled down, took hold with its suckers, and crept along.

The tail was very easily detached from the body and would continue swimming for some time with a wriggling motion. Whenever an actively detached tail came in contact with the substratum, it ceased wriggling and alternately extended and contracted as if it were still attached to a living cercaria. One of the detached tails kept up active movement for over fifteen minutes and then was stopped by the drying up of the water around it.

Small thin walled cyst containing tailless individuals of *Cercaria polyadena* were found scattered in with the material preserved for study (Fig. 71). It is probable that these cysts were formed after the liver was removed from the snail, and that *Lymnaea reflexa* is not the secondary intermediate host of this species. The formation of the cyst was not observed but that the glands were ready for secretion is shown by the fact that the extrusion of the cystogenous material was observed in one individual that was flattened under a cover slip. The cysts were round and varied in diameter from 0.15 mm. to 0.16 mm., and the transparent cyst wall varied in thickness from 0.005 to 0.007 mm.

*Cercaria polyadena* (Fig. 70) is very variable in shape, living specimens changing from 0.12 mm. when contracted to 0.30 mm. at greatest extension. When most contracted the tail may be less than one-half the body length, but when the animal was swimming it reaches to 0.30 mm. The average measurements of five mounted individuals in about the state of contraction of the figure, give the length of 0.18 mm., the width of 0.07 mm., the length of the tail 0.12 mm. and its width 0.017 mm. The tail is attached in a groove on the ventral surface of the posterior end, and altho it is small for the size of the body it is relatively larger than in *Cercaria isocotylea*.

The oral sucker has an average diameter in mounted specimens of 0.040 mm. and the spherical acetabulum which is three-fifths of the distance from the anterior to the posterior end is 0.025 mm. wide.

In the dorsal wall of the oral sucker is set a stylet like that of *Cercaria isocotylea*. It is 0.028 to 0.03 mm. in length and thickened as in the other species.

The whole surface of the body is set with tiny spines contained entirely within the cuticula and not set in rows; these thin out somewhat in the postacetabular region.

Two groups of voluminous ducts pass up dorsad to the oral sucker from the stylet glands, which fill most of the space from the acetabulum to the pharynx. The diameter of one of these ducts is from 0.004 mm. to 0.005 mm. The stylet glands are divided into two groups of from ten to twelve in a group, and the individual glands vary in length from 0.017 to 0.022 mm., and in width from 0.010 mm. to 0.014 mm.

Cystogenous glands are present both on the dorsal and ventral sides of the body from the pharynx to the posterior end.

In *Cercaria polyadena* the oral cavity is followed by a short pre-pharynx 0.015 mm. in diameter. No traces were seen either of the esophagus or the intestinal ceca.

The excretory bladder is bicornuate and the excretory pore is located dorsally at the base of the tail. The two horns of the vesicle extend up to the posterior lateral margins of the acetabulum, and each receives a small vessel. This receives a long vessel from the region of the pharynx and a short vessel from the posterior end. The lining of the vesicle is formed of a layer of slightly flattened cuboidal epithelial cells with prominent nuclei and well defined cell boundaries.

The anlage of the reproductive organs is not differentiated into its individual parts. It is represented by an elongate s-shaped mass of nuclei lying dorsad to the acetabulum and extending backward beyond its posterior margin.

*Cercaria polyadena* and *Cercaria isocotylea* are very much alike and form the nucleus of a group the members of which present such uniformity of characters that they must be considered to be related. The name Polyadenous cercariae may then be proposed as the name of a natural group the members of which correspond closely to *Cercaria polyadena*.

The following are the characters of the Polyadena cercariae:

1. Development in gastropods in elongate sac-shaped sporocysts.
2. Tail slender and less than the body length except when very much extended.

3. Acetabulum back of the middle of the body and smaller than the oral sucker.

4. Stylet about 0.030 mm. in length, six times as long as broad, and with a thickening one-third of the distance from the point to the base.

5. Stylet glands, six or more on each side between the acetabulum and the pharynx.

6. Excretory bladder bicornuate.

7. Very short prepharynx and small pharynx present. Esophagus when developed short to of medium length. Intestinal ceca (when present reaching to posterior end of body).

Two European fresh-water cercariae, *Cercaria limnaeae ovatae* von Linstow and *Cercaria secunda* Ssinitzin, without doubt belong to this group. They both agree in all known particulars with the characterization given above. No mention is made, however, in von Linstow's (1884) account of stylet glands.

There are definite specific differences between the four forms which constitute the Polyadenous cercariae. Of the two American forms *Cercaria polyadena* has a larger body and tail, a smaller oral sucker, and a larger number of stylet glands. *Cercaria limnaeae ovatae* is the largest of the group, has much larger suckers than any of the others, and is developed in larger sporocysts. The closest correspondence is between *Cercaria polyadena* and *Cercaria secunda* Ssinitzin. These two species are certainly very closely related. *Cercaria secunda* is, however, larger in size and has slightly larger suckers and fewer stylet glands than *Cercaria polyadena*.

Some suggestion can be made in regard to the type of adults into which the cercaria of this group develop. *Cercaria limnaeae ovatae* has been assigned to *Opisthioglyphe rastellus* (Lühe, 1909:108) and Ssinitzin (1905) suggests that *Cercaria secunda* may be the larva of a *Plagiorchis* species. It would seem probable from the above facts and the structure of the excretory and digestive systems that the Polyadenous cercariae belong in Lühe's subfamily *Plagiorchiinae* which contains *Opisthioglyphe* as well as *Plagiorchis*. The further development of the two American forms is entirely unknown.

#### CERCARIAE ORNATAE

In 5 per cent. of the specimens of *Physa gyrina* from Rockford, Illinois, the body contained a tangled mass of elongated, orange pigmented sporocysts. The tubes did not branch, they were of varying



caliber and club-shaped ends protruded from the mass. They were very much twisted together and none of the individual sacs were disentangled without breaking. The jutting ends moved slightly, swaying backward and forward.

Thruout their whole length the sporocysts (Fig. 77) were stuffed with cercariae of different ages, and mature forms in large numbers wormed out of the broken places in the sporocysts. The swimming movement of the cercaria offered nothing peculiar and since the oral sucker did not appear to function, creeping was not very effective. The name *Cercaria hemilophura* is proposed from the fact that a fin-like projection extends for half the length of the tail.

*Cercaria hemilophura* (Fig. 76) is oval elongate in shape and widest at about the middle. The average length in well extended mounted specimens is 0.38 mm. and the width 0.14 mm., with a thickness of about one-half the width.

The tail at average extension is about the length of the body, 0.36 mm. being the average in toto mounts and with a width of 0.048 mm., but it can be extended to almost twice that length. Along the ventral surface of the posterior half of the tail extends a fin-like projection, which at its widest is about half the width of the tail.

The oral sucker has a length of 0.065 mm. and the acetabulum, which is just back of the middle of the body, has a diameter of 0.049 mm.

The stylet (Fig. 75) is small, tapers regularly to a point and has no thickened region. It measures 0.020 mm. in length and 0.005 mm. in width at its base.

The whole surface of the body is covered with very small cuticular spines pointing backward, which are very dense in the preacetabular region but thin out slightly posteriorly. They are contained entirely within the thickness of the cuticula and have a length of from 0.0055 mm. to 0.0065 mm.

The whole body contains large numbers of small cystogenous glands filling almost all the available space.

Stylet glands could not be distinguished.

The digestive system of *Cercaria hemilophura* is very clearly differentiated. The oral cavity is followed by a very short prepharynx and a good sized pharynx 0.033 mm. in diameter. From the pharynx a large esophagus reaches back almost to the acetabulum. The esophagus is thin walled but the intestinal ceca are lined with cuboidal cells which at this stage fill most of the lumina.

It was possible in many cases to trace the branches of the excretory system to the flame cells. The bladder is club-shaped, extending about three-fourths of the distance from the posterior end to the acetabulum,



and widens slightly at its anterior end. Into it flow two vessels from the region of the oral sucker on each side, which are met by vessels from the posterior end at the region of the acetabulum. Small branches lead from the flame cells and connect with these branches. Figure 76 shows the excretory system of *Cercaria hemilophura*.

The anlagen of the reproductive organs are represented by a two lobed mass of nuclei dorsal to the acetabulum.

According to Lühe's classification of the Xiphidiocercariae *Cercaria hemilophura* would belong with the group *Cercariae ornatae*. He gives the following definition for this group:

"Distome Cercarien mit Bohrstachel, deren schlanker Ruderschwanz einen Flossensaum besitzt."

He included in this group *Cercaria ornata* La Valette and *Cercaria prima* Ssinitzin. This is certainly not a natural subdivision, since the three forms are very different in other structures. The presence of such a character as the "Flossensaum" hardly forms the basis for a natural group. Since it has been developed also in such widely different groups as the monostomes and the echinostomes. At the present state of our knowledge it seems impossible to relate *Cercaria hemilophura* to any natural group. Neither is there any suggestion as to the further development of this species.

#### MICROCOTYLOUS CERCARIAE

The tissue above the gills in three out of thirty-six specimens of *Campeloma subsolidum* from Hartford, Conn., was heavily infected with oval thin-walled sporocysts. The sporocysts had granular, somewhat opaque walls, varied in shape from almost round to elongate oval, and contained small cercariae in different stages of development. None of the cercariae were fully mature and none were found free in the tissues of the host. There was little movement of the cercariae either within the sporocysts or when freed. I propose the name *Cercaria leptacantha* for this species on account of the small size of the stylet.

The sporocysts (Fig. 81) varied from 0.26 mm. to 0.41 mm. in length and from 0.15 mm. to 0.26 mm. in width.

The body of *Cercaria leptacantha* (Fig. 80) is oval elongate and almost circular in cross-section. The average measurements of five well extended mounted specimens are 0.12 mm. in length and 0.063 mm. in width. The tail is not fully developed still remaining as a direct continuation of the body and having little power of movement. It is less than the length of the body and slender, averaging 0.081 mm. in length and 0.016 mm. at its greatest width.

In none of the individuals studied were the suckers fully developed or functional. The oral sucker shows a beginning of a mouth cavity but the acetabulum is merely a rounded off mass of embryonic nuclei. In mounted specimens the oral sucker averages 0.027 mm. in diameter and the acetabulum, which is back of the middle of the body, has a width of 0.024 mm.

On the surface of living specimens of *Cercaria leptacantha* were scattered highly refractive round globules of different sizes, which appeared like water or oil droplets. These bodies, which resemble the concretions in the excretory systems of certain cercariae, were so prominent that they could be seen thru the walls of the sporocysts, but disappeared in the preservation of the material.

The small characteristic stylet (Fig. 79) is 0.011 mm. to 0.13 mm. in length, and 0.0025 mm. in thickness at its base.

Two kinds of glands were present in *Cercaria leptacantha*. The first type consists of small irregular shaped bodies with granular contents at the anterior lateral margins of the acetabulum. The other type are almost clear globlet shaped stylet glands, four on each side arranged along the body lateral to the acetabulum, with ducts from their outer margins leading up to the cephalic spine. No ducts were found for the first type of gland, but from their granular contents they may be cystogenous in character.

The digestive system of *Cercaria leptacantha* is represented only by a short prepharynx and a small pharynx 0.09 mm. in diameter.

Of the excretory system only the elongate, club-shaped bladder can be distinguished.

The anlage of the reproductive organs is represented merely by a large mass of small nuclei dorsal and posterior to the acetabulum.

*Cercaria leptacantha* belongs to a group of very small cercariae which Lühe (1909:196) calls Cercariae Microcotylae. It is possible that they form a natural group. They are, however, so insufficiently known that no final judgment can be passed on their relationships. At present it seems best to follow Lühe in considering them a provisional group, with *Cercaria microcotyla* Filippi as the type and the following characteristics.

1. Developed in gastropods in round or oval sporocysts which are seldom more than twice as long as wide.
2. Cercariae under 0.2 mm. in length.
3. Acetabulum back of the middle of the body and smaller than the oral sucker.

4. Stylet glands not more than four on each side and arranged in rows on each side of the acetabulum.

5. Digestive system undeveloped except for a short prepharynx and a small pharynx.

Three European and three Egyptian cercariae are sufficiently known to be included with any certainty in this group. The European forms are *Cercaria pugnax* La Valette, *Cercaria microcotyla* Filippi, and *Cercaria subulo* Pagenstecher (for description of these forms see Lühe, 1909: 196-198), and the Egyptian forms are *Cercaria celluosa* sp. inq., *Cercaria pusilla* sp. inq., and *Cercaria exigua* sp. inq. all described by Looss (1896:227-232). Insufficiently known forms which from their small size and the shape of the sporocysts may belong to this group are *Cercaria chlorotica* Diesing, *Cercaria alba* Ercolani, and *Cercaria punctum* Ercolani. *Cercaria parva* Ercolani in which the oral sucker is smaller than the acetabulum agrees in its other characters with the members of this group.

The Microcotylous cercariae are best distinguished from each other by the size and shape of their stylets. *Cercaria leptacantha* agrees most closely with the Egyptian species *Cercaria exigua*. It is larger than this species however, the suckers differ in size and the ratio of size, and the stylets differ in size and shape.

Only one suggestion is found in regard to the adults of this group. Looss (1896:232) considers that the three cercariae of this type described by him may belong to some small distomes found in Egypt in the intestines of chameleons and lizards. He offers no particular grounds for this hypothesis.

Last will be considered a form of the Xiphidiocercariae which seems to be different from all forms previously described. The livers of three out of ninety-one specimens of *Physa anatina* from Manhattan, Kansas, were infected with sausage-shaped sporocysts (Fig. 72) which contained cercariae in different stages of development. I propose for this species the name *Cercaria brevicaeca* from the fact that the intestinal ceca are very short.

*Cercaria brevicaeca* moved clumsily and irregularly while swimming and did not creep by aid of its suckers. The infection was very slight and all the observations were made from living specimens. None of the cercariae were observed to live more than two or three hours after removal from the snail.



*Cercaria brevicaeca* (Fig. 74) was elongate oval in shape and its tail, which was very easily lost, had about the same length as the body. At average extension the body had a length of about 0.30 mm. and a width of 0.14 mm. The tail did not change its shape very greatly and ranged in length only from 0.22 mm. to 0.38 mm. with a width at its base of 0.038 mm. It was attached in a groove in the ventral side of the posterior end and when contracted had a tendency to curl at its tip.

The oral sucker of *Cercaria brevicaeca* had an average diameter of 0.082 mm. and the acetabulum, which is just back of the middle of the body, was slightly larger, 0.087 mm.

The stylet (Fig. 73) had a length of 0.018 mm. and was slightly thickened 0.007 mm. from its point.

The body back to the acetabulum was covered thickly with rows of very tiny spines.

In the region between the acetabulum and the pharynx were two clumps of from ten to twelve stylet glands, varying in length from 0.026 mm. to 0.035 mm. and in width from 0.018 mm. to 0.025 mm. The ducts from these glands united into two groups one on each side which passed dorsad of the oral sucker to open beside the stylet.

Almost every bit of available space behind the pharynx was filled with cystogenous glands, which from the surface appeared as round, granular bodies 0.014 mm. to 0.017 mm. in diameter.

The oral cavity was followed by a short prepharynx and a small pharynx, 0.030 mm. in diameter. The short, narrow esophagus divided just in front of the acetabulum into short intestinal ceca which did not reach beyond the acetabulum. The lumina of the ceca showed only as irregular, elongate spaces in the granular contents.

Of the excretory system only the peculiarly shaped vesicle could be made out. This was composed of a pyriform median portion, and two more narrow lateral parts which almost completely surrounded the acetabulum. The pore opened dorsad at the base of the tail.

No cercariae were found in the literature closely corresponding with *Cercaria brevicaeca*. Especially unique is the shape of the excretory vesicle.

#### THE CLASSIFICATION OF THE CERCARIAE

At the present state of our knowledge it is impossible to fit most of the cercariae into the general trematode classification, for, except in those forms like the echinostomes or the amphistomes, where the larvae are much like the adults, or in a group like the family *Gorgoderinidae*, where the life histories of several species have been worked out, little



is definitely known of the relation of the cercariae types to the adults. Therefore for convenience it has seemed advisable to build up a tentative classification of the cercariae, treating them almost as if they were an independent class of the animal kingdom. Of necessity such a classification must be based pretty largely on superficial characters. As our knowledge increases wherever possible natural groups must be substituted for the artificial, and as more and more larvae are connected with the adults, the classification of the cercariae will gradually be merged with that of the adults.

In order to understand clearly the classification that has been made for larval trematodes, a careful analysis of the characters used for comparison must be made. Cercarial characters can be roughly divided into two main groups: (1) adult characters, and (2) larval characters. By adult characters of a cercaria are meant those which foreshadow adult structure. It is by the use of these characters as a basis that the greatest progress in natural classification can be made, since the more the adult characters are developed, the more will the cercariae resemble the adults, as in amphistome and echinostome larvae. For example the digestive and the excretory systems of the cercariae of these groups are much like those of the adult. Sometimes in the larva definite specific peculiarities of the adult can be distinguished in detail. Thus Looss (1896:192-197) in attempting to prove by morphological comparison that *Monostomum verrucosum* Froel (*Notocotyle triseriale* Diesing) and *Cercaria imbricata* Looss belong to the same species, advances as his strongest argument, that in the mature cercaria are found around the excretory pore plications arranged as the rays of a circle like those found in the adult. A combination of adult characters will often give a clue to the family or even in a few cases to the genus to which the cercaria belongs. Allowance must be made however for the fact that adult characters may be somewhat modified in the development of the cercaria. For example the loss of the tail modifies the excretory system, and changes in shape and proportion of the body change considerably the relative lengths of the different parts of the digestive system.

Larval characters of cercariae may be defined as those which are not carried over into adult life. Many structures are developed to meet the exigencies of larval conditions, and are merely temporary. In many cercariae much dependence must be placed on such characters in classification, for often as in the forked-tailed and stylet cercariae, adult characters are very little differentiated and the whole structure is very largely dominated by larval characteristics. This brings up the question as to how far such characters can be considered as expressing relationship. Like structures in cercariae either show relationship or

convergence due to adaptations to similar environments. Such an adaptation as the development of a boring spine which occurs in cercariae widely different in other characters, can hardly be considered as showing close relationship. When, however, cercariae are very similar in a number of larval characters such likeness can hardly be ascribed to convergence, and even if adult characters are not sufficiently developed for comparison, such forms can with reasonable certainty be placed together in natural groups.

Another question which must be considered in classifying certain cercariae, is whether the larvae of closely related adults might not be different on account of modifications in larval life. From consideration of conditions in other groups this would seem very possible. The little evidence that we have, however, seems to indicate that the cercariae of closely related forms are more alike than the adults. Lühe (1909:175) suggests this as one reason for the small numbers of cercariae known in comparison with the adults.

“Vielfach sint übrigens die Cercarien verschiedener Trematoden-Arten einander so ausserordentlich ähnlich, dass ihre sichere Bestimmung, wenigstens bei unseren jetzigen Kenntnissen, nicht möglich ist, and manche alte Art-namen haben dadurch die Bedeutung von Gruppen-statt von Artbezeichnungen gewonnen.”

The statement of these problems shows how merely tentative at the present state of our knowledge must be considered any classification of cercariae.

The most extensive classification of the cercariae is that of Lühe (1909:173-210). His main subdivisions are for the most part based on the recognition of the relationship of the cercariae to the larger recognized adult groups. In the subdivision of the distome cercariae, however, his classification is to a considerable extent purely artificial, being based on the character of the tail. A summary of Lühe's classification follows.

#### LUHE'S CLASSIFICATION OF THE CERCARIAE

- A. Lophocercariae  
Cercariae with longitudinal projections along the sides of the body.  
Ex. *Cercaria crista* La Valette.
- B. Gasterostome cercariae  
Two long projections from the end of the body. Mouth opening in the middle of the ventral surface. Intestine simple sac-shaped.  
Ex. *Bucephalus polymorphus* Baer.
- C. Monostome cercariae  
Ventral sucker lacking. Ex. *Cercaria urbanensis* Cort.

- D. Amphistome cercariae  
Ventral sucker at the posterior end of the body. Ex. *Cercaria inhabilis* Cort
- E. Distome cercariae  
Ventral sucker some distance in front of the posterior end of the body.
1. Cystocercous cercariae  
Base of the tail forms a space into which the body can be drawn. Ex. *Cercaria macrocerca* Filippi.
  2. Rhopalocercous cercariae  
Tail having as great or greater width than the body. Ex. *Cercaria isopori* Looss.
  3. Leptocercous cercariae  
Tail straight, slender, and narrower than the body.
    - a. Gymnocephalous cercariae  
Anterior end rounded, without stylet or boring spine. Ex. *Cercaria megalura* Cort.
    - b. Echinostome cercariae  
Anterior end with a collar and crown of spines. Ex. *Cercaria trivolvis* Cort
    - c. Xiphidiocercariae  
Anterior end with stylet. Ex. *Cercaria isocotylea* Cort.
  4. Trichocercous cercariae  
Tail set with spines. Ex. *Cercaria setifera* Moulinié.
  5. Furcocercous cercariae  
Tail forked at its end. Ex. *Cercaria douthitti* Cort.
  6. Microcercous cercariae  
Tail stumpy. Ex. *Cercaria brachyura* Lespés.
  7. Cercariaeae  
Tail entirely undeveloped. Ex. *Leucochloridium paradoxum* Carus.
  8. Rattenkönigcercariae  
Cercariae with tails joined, forming a sort of colony.

In the present state of our knowledge it seems to me that for the comparison of forms, no general grouping can be suggested which will be of more help to workers. It must be recognized, however, that many of the groups are purely artificial. The Gymnocephalous cercariae have little in common but negative characters, and the stylet cercariae form a very heterogeneous mass. These and other groups are merely temporary arrangements for convenience and must be split up or rearranged into more natural groups as soon as our knowledge permits.

Marie Lebour (1912) tried to substitute for Lühe's classification one based on other characters. According to her classification the cercariae are divided into two large groups depending on whether they develop in rediae or sporocysts, and within these groups are formed small groups of apparently related forms. As an attempt to form closely related groups this work is very suggestive, but as a working classification it has very limited value. In the first place there is little evidence for the belief that development in sporocysts or rediae expresses fundamental relationship. Such widely divergent forms develop from sporocysts as *Bucephalus*, tailless cercariae, stylet cercariae, etc. The most important part of Miss Lebour's work is her attempt to build up natural groups of closely related forms centering around some well known species, as for instance, her *Spelotrema* group centering around *Spelotrema excellens*. The following is the essential part of Lebour's classification.

#### Lebour's Classification of the Cercariae

##### A. Gasterostomata

Cercariae develop in sporocysts. Mouth at middle of ventral surface. Ex. *Bucephalous polymorphus* Baer.

##### B. Prostomata

Mouth at anterior end.

##### 1. Distome cercariae

Two suckers.

##### a. Cercariae developed in sporocysts.

##### (1) Gymnophallus group

Cercaria tailless. Ex. *Cercaria glandosa* Lebour.

##### (2) Fork-tailed cercariae

Tail forked at its end. Ex. *Cercaria douthitti* Cort.

##### (3) *Spelotrema* group

Free swimming stage with stylet. Encysted cercaria tongue-shaped, covered with spines, with long prepharynx and esophagus, short ceca not reaching to the end of the body. Ex. *Cercaria* of *Spelotrema excellens*. (?)

##### (4) Stumpy-tailed cercariae

Tail broad and stumpy. Ex. *Cercaria brachyura* Lespés.

##### (5) Lepodora group

Body covered with spines. Intestinal ceca reaching nearly to posterior end of body. Tail



present in very young forms, but cast off before encystment, which takes place within the sausage-shaped sporocysts. Ex. *Cercaria* of *Lepodora rachiaea*. (?)

b. *Cercariae* developed in rediae.

(1) *Cercariae neptuneae*

Tail very thick and large, two eye-spots present. Excretory vesicle very thick walled. Ex. *Cercaria neptuneae* Lebour.

(2) *Acanthopsolus* group

Two eye-spots, intestinal ceca reaching nearly to the end of the body, thin tail developed in young forms but cast off before it is full grown. Ex. *Cercaria* of *Acanthopsolus lageniformis*. (?)

(3) *Echinostomum* group

*Cercariae* with anterior collar and crown of spines. Ex. *Cercaria trivolvis* Cort.

2. Monostome group

One sucker present. Ex. *Cercaria urbanensis* Cort.

It is in attempts to join a few closely related cercariae into groups which are probably natural, rather than in further broad generalizations which must be based on artificial characters, that hope for advance in the classification of cercariae lies. As more and more life-histories are worked out, such groups can be fitted into their place in the adult classification, until the relationship of all the cercariae groups to the adults will be known.

\*      \*

Note. All of the species of *Cercaria* discussed in detail in this paper were originally described in my preliminary report (Cort, 1914).

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## EXPLANATION OF PLATES

Unless otherwise stated all figures are drawn with a camera lucida.

The lettering on some toto drawings of the cercariae was omitted by error. The descriptions in the text will be sufficient to make the structure clear.

## ABBREVIATIONS USED

<i>ab</i>	annular bands of muscle	<i>lc</i>	large central cells of tail
<i>ac</i>	acetabulum	<i>ls</i>	lobes of snail's liver
<i>acr</i>	anterior collar of redia	<i>ml</i>	muscle layer
<i>bp</i>	birth pore of redia	<i>n</i>	nervous tissue
<i>cg</i>	cystogenous glands	<i>os</i>	oral sucker
<i>ccg</i>	cephalic glands	<i>p</i>	pigmentation
<i>cm</i>	cystogenous material	<i>pb</i>	pharyngeal bulb
<i>cr</i>	cercaria in redia	<i>pc</i>	parenchymatous cells
<i>dc</i>	ducts of cephalic glands	<i>pl</i>	pigment line
<i>e</i>	eye-spot	<i>pr</i>	pharynx of redia
<i>es</i>	esophagus	<i>ra</i>	reproductive anlage
<i>ex</i>	excretory system	<i>s</i>	stylet
<i>exv</i>	excretory vessel	<i>sc</i>	cercaria in sporocysts
<i>gb</i>	germ ball	<i>sg</i>	stylet glands
<i>i</i>	intestinal cecum of cercaria	<i>sw</i>	wall of sporocyst
<i>ir</i>	intestine of redia	<i>vt</i>	excretory vessels of tail
<i>la</i>	locomotor appendages of redia		

## EXPLANATION OF PLATE

- Figures 1 to 4. Free hand drawings of stages in the process of encystment of *Cercaria urbanensis*. X about 70.
- Fig. 5. Mature *Cercaria urbanensis*, ventral view. Cystogenous glands not shown. X 140.
- Fig. 6. Posterior locomotor projection of *Cercaria ephemera*. From Ssnitzin.
- Fig. 7. Posterior locomotor projection of *Cercaria imbricata*. From Looss.
- Fig. 8. Posterior locomotor projection of *Cercaria urbanensis*. X 433.
- Fig. 9. Cross section of the tail of *Cercaria urbanensis*. X 433.
- Fig. 10. Immature redia of *Cercaria urbanensis*... X 88.
- Fig. 11. Mature redia of *Cercaria urbanensis*. X 88.
- Fig. 12. Mature redia of *Cercaria urbanensis*, showing constrictions. X 44.
- Fig. 13. Cross section of immature redia of *Cercaria urbanensis*. X 433.

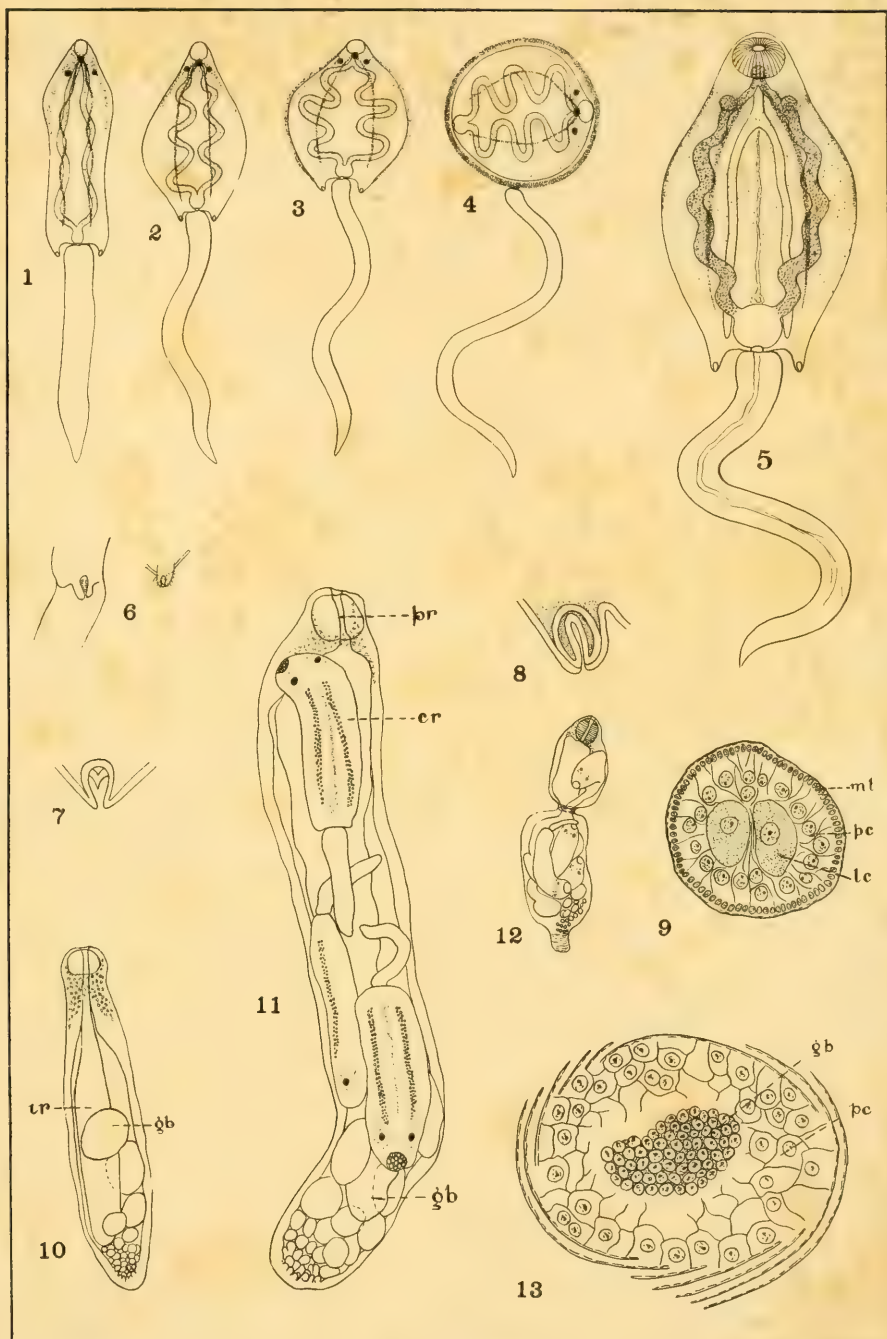


PLATE I





## PLATE II

## EXPLANATION OF PLATE

- Fig. 14. Immature redia of *Cercaria urbanensis*. X 88.  
Fig. 15. Redia of *Cercaria inhabilis*. X 88.  
Fig. 16. Mature *Cercaria inhabilis*, ventral view. Cystogenous glands not shown.  
X 88.  
Fig. 17. Cross section of *Cercaria inhabilis* in region of eye-spots. X 195.  
Figures 18 to 21. Anterior body region of different stages of *Cercaria inhabilis*,  
showing changes in pigmentation. X 140.  
Fig. 22. Cross section of the tail of *Cercaria inhabilis*. X 433.

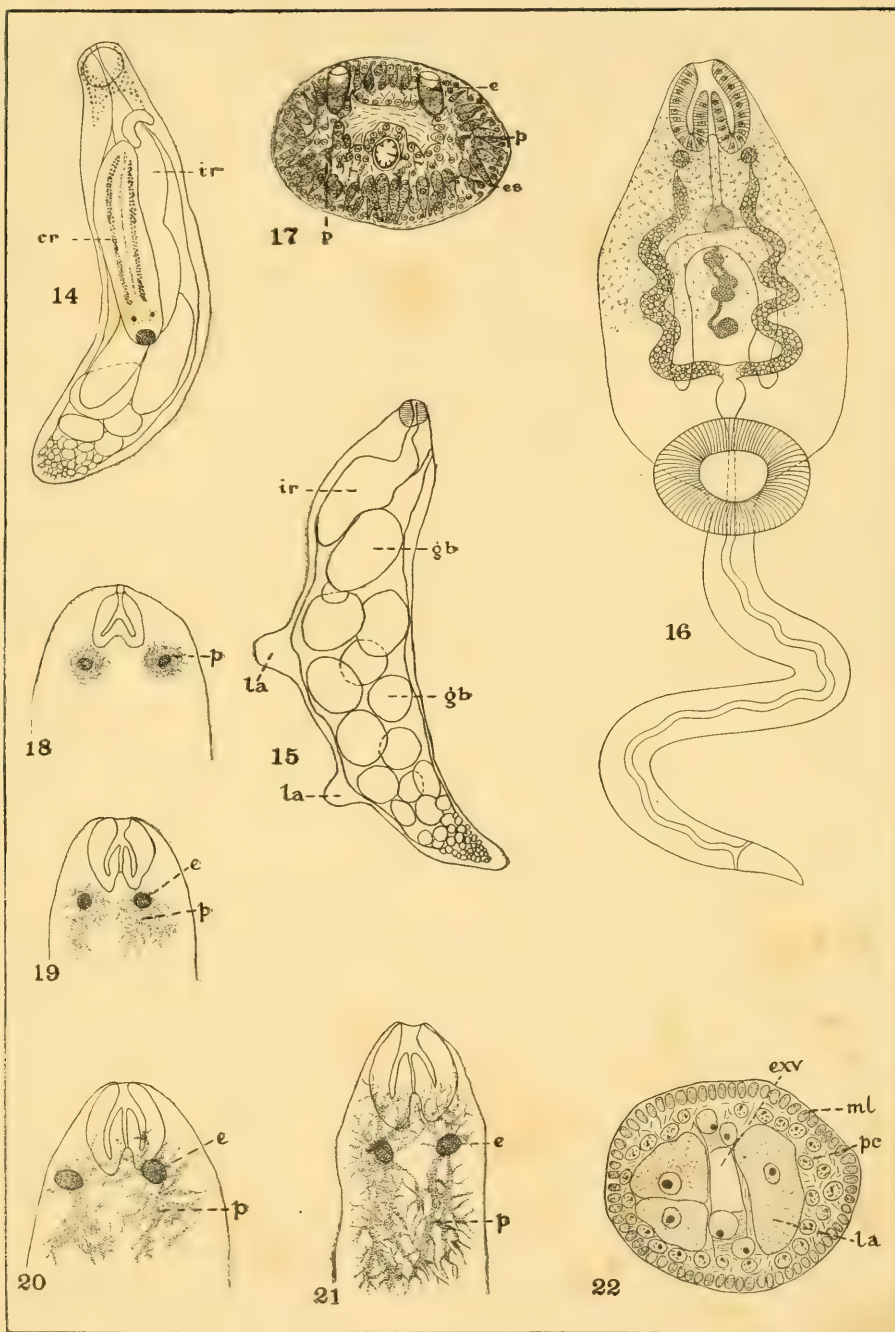


PLATE II





## PLATE III

## EXPLANATION OF PLATE

- Fig. 23. Mature *Cercaria diastrophæ*, dorsal view. Cystogenous glands not shown. X 88.
- Fig. 24. Free hand drawing of *Cercaria diastrophæ* from the side. X 75.
- Fig. 25. Redia of *Cercaria diastrophæ*. X 88.
- Fig. 26. *Cercaria caryi*, ventral view. From Cary's material. X 140.
- Fig. 27. *Cercaria megalura*, ventral view. From Cary's material. X 140.
- Fig. 28. *Diplodiscus temporatus*, ventral view. From Cary's experimental tadpoles. X 140.

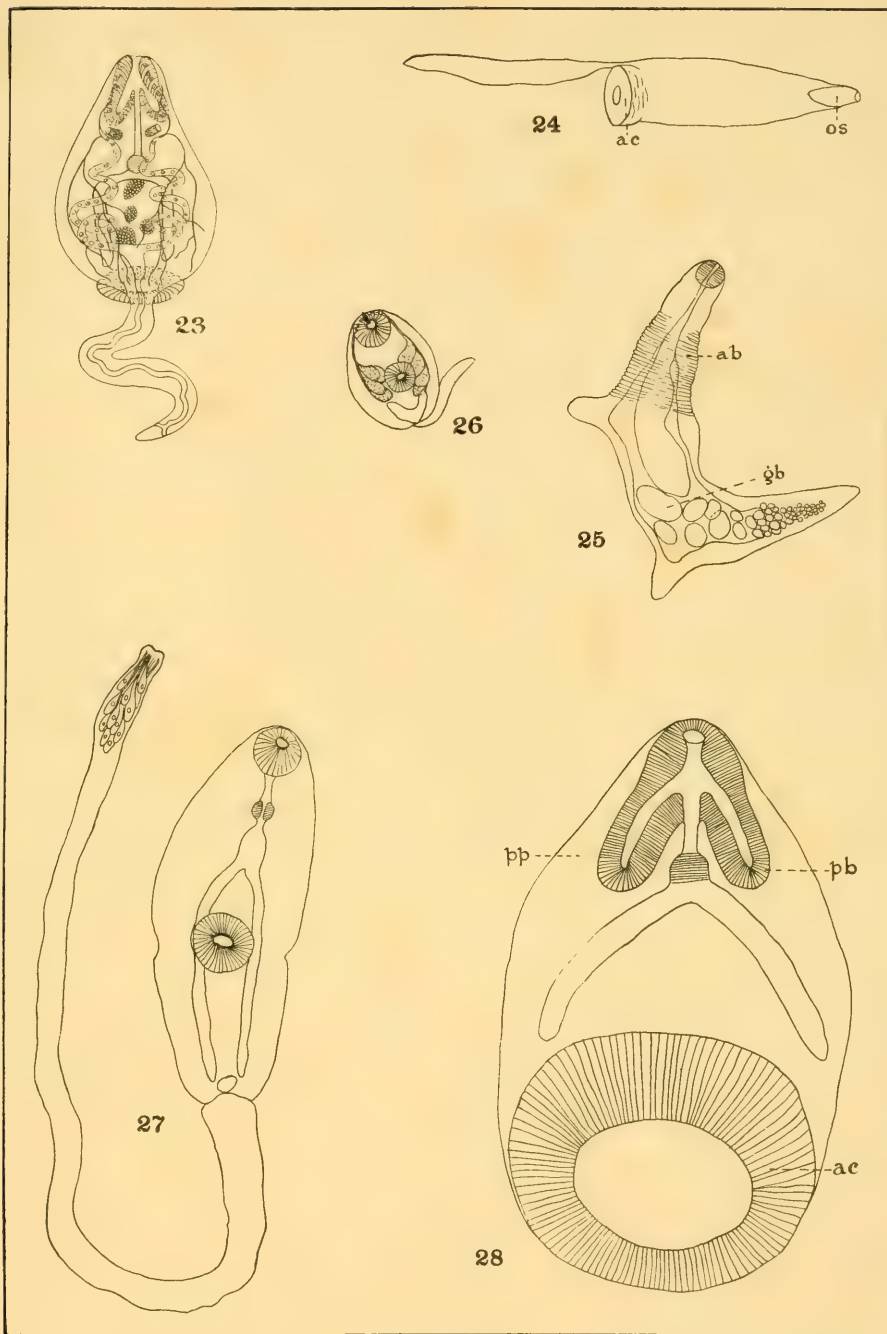


PLATE III





## PLATE IV

## EXPLANATION OF PLATE

- Fig. 29. *Cercaria megalura* before the extrusion of cystogenous material, ventral view. X 195.
- Fig. 30. *Cercaria megalura* after the extrusion of cystogenous material, ventral view. X 195.
- Fig. 31. Mature redia of *Cercaria megalura*. X 88.
- Fig. 32. Cross section of tail of *Cercaria megalura*. X 433.
- Fig. 33. Cross section of *Cercaria megalura* before the extrusion of cystogenous material. X 276.
- Fig. 34. Cross section of *Cercaria megalura* after the extrusion of cystogenous material. X 276.
- Fig. 35. Cross section of immature redia of *Cercaria megalura*. X 433.
- Fig. 36. Immature redia of *Cercaria megalura*. X 88.

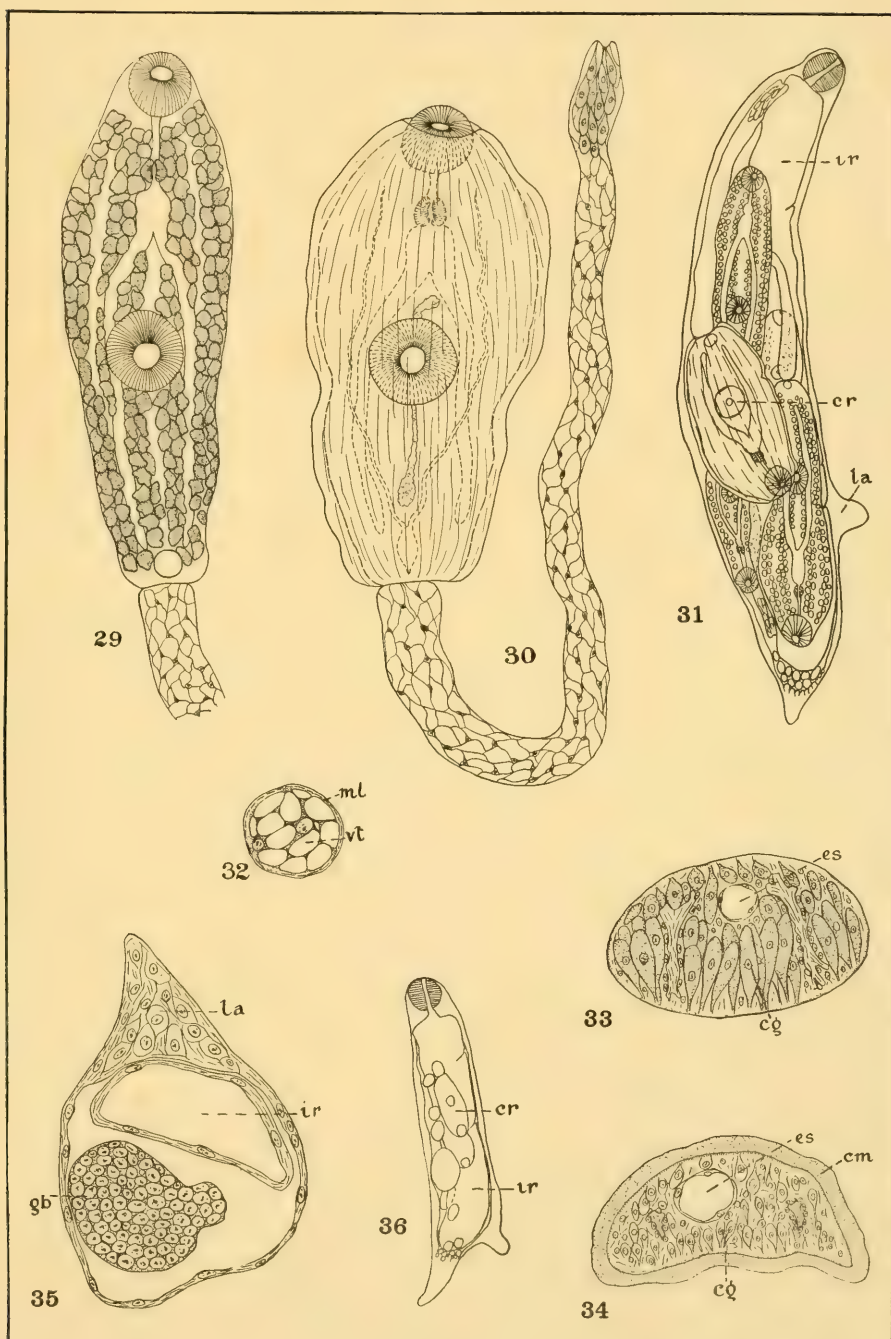


PLATE IV

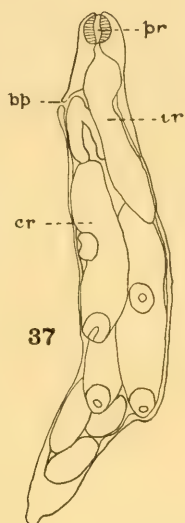




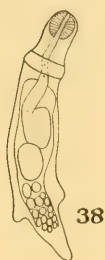
## PLATE V

## EXPLANATION OF PLATE

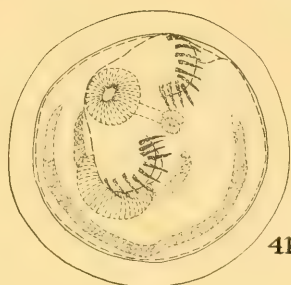
- Fig. 37. Mature redia of *Cercaria trivolvis*. X 88.  
Fig. 38. Immature redia of *Cercaria trivolvis*. X 88.  
Fig. 39. Mature *Cercaria trivolvis*, ventral view. Cystogenous glands not shown.  
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Fig. 40. *Cercaria rubra* freed from cyst, ventral view. X 195.  
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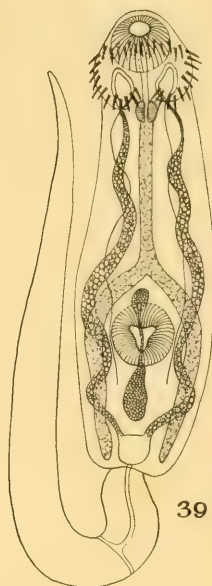
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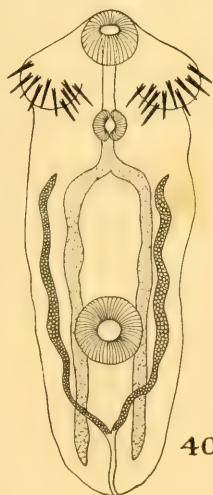
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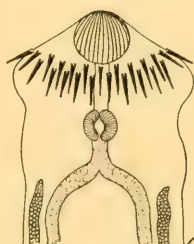
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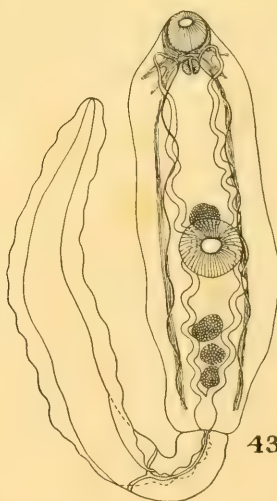
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## PLATE VI

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- Fig. 44. Immature relia of *Cercaria reflexae*. X 88.  
Fig. 45. Mature redia of *Cercaria reflexae*. X 44.  
Fig. 46. Nervous system of immature redia of *Cercaria reflexae*. X 276.  
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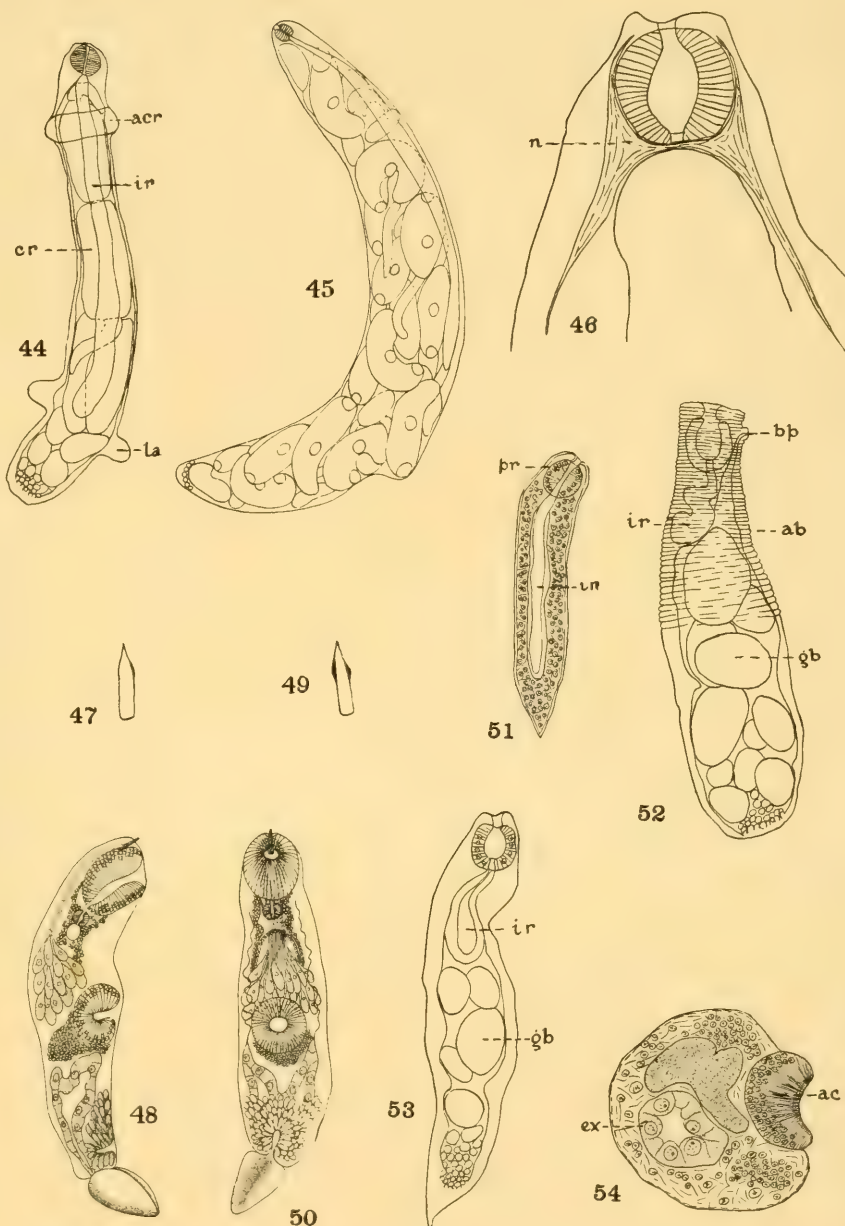


PLATE VI





## PLATE VII

## EXPLANATION OF PLATE

- Fig. 55. *Cercaria douthitti*, ventral view. X 195.  
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Fig. 67. Stylet of *Cercaria isocotylea* from ventral and side view. X 433.  
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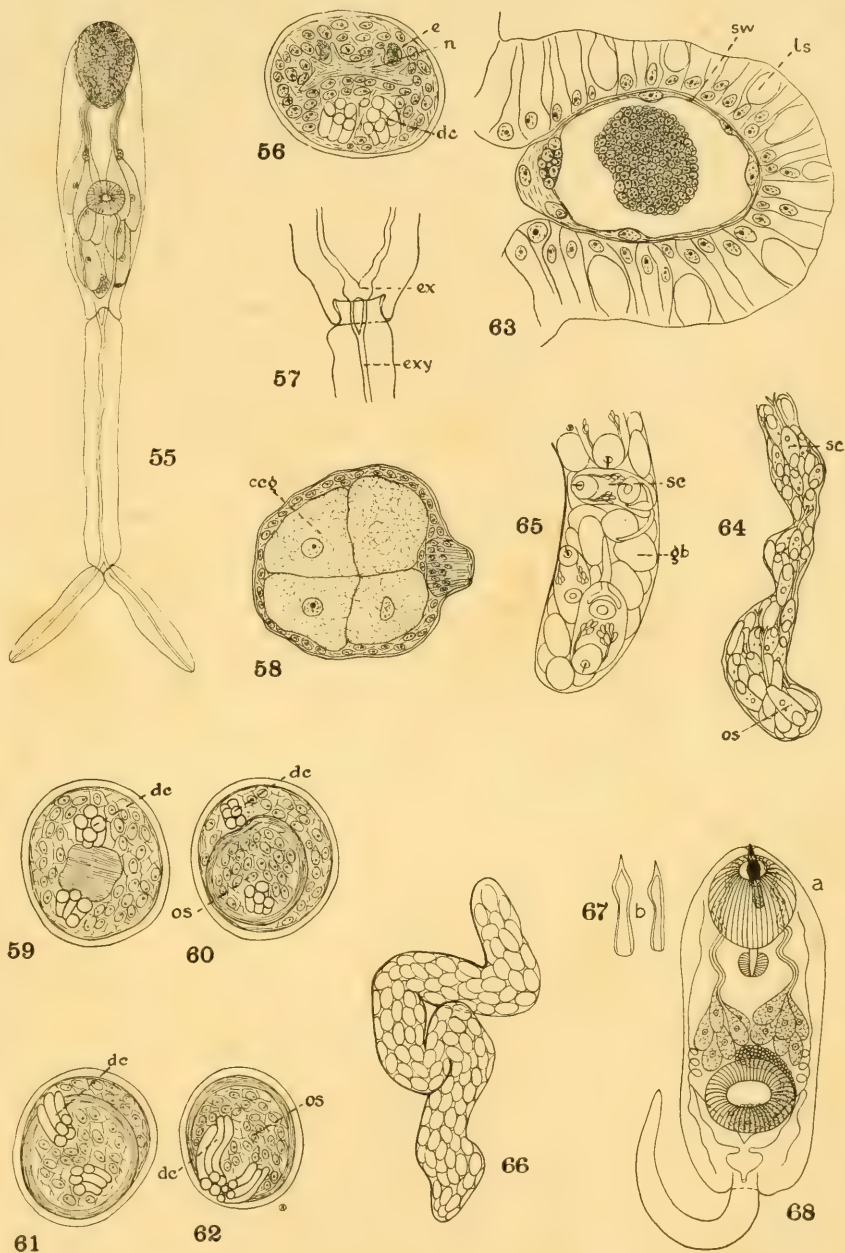


PLATE VII





## PLATE VIII

## EXPLANATION OF PLATE

- Fig. 69. Stylet of *Cercaria polyadena*, ventral view. X 433.  
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